EVALUATION OF THE EFFECT OF DIETARY FORAGE AND CONCENTRATE LEVELS ON THE FATTY ACID PROFILE OF BISON TISSUE

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Abstract

The effects of feeding strategy on subcutaneous, perirenal adipose tissue and ribeye (*longissimus dorsi*) muscle fatty acid profiles were evaluated from 60 bison (*Bison bison*) bulls from Western Canada. Treatments included Forage Fed (n=19); short term concentrate feeding, <90 Day (n=9); mixed forage and concentrate feeding, 50:50 Forage:Grain (n=20); and Feedlot Finishing (n=12), and were analyzed for interactions and main effects between treatment and tissue type. Saturated fatty acids were found in larger ($P<0.05$) proportions within perirenal tissue for all treatments. Polyunsaturated fatty acids were concentrated ($P<0.05$) in the intramuscular tissue. Polyunsaturated fatty acid content was greater ($P<0.05$) in Forage Fed and 50:50 Forage:Grain than in <90 Day or Feedlot Finishing treatments. The polyunsaturated to saturated fatty acid ratio was greatest ($P<0.05$) for Forage Fed followed by 50:50 Forage:Grain, with <90 Day and Feedlot Finishing treatments having the lowest ratio. Linoleic acid content within intramuscular tissue was greatest ($P<0.05$) in the 50:50 Forage:Grain followed by the <90 Day treatment, with the Forage Fed group being intermediate, and the Feedlot Finishing being the lowest ($P<0.05$). Subcutaneous tissue contained more ($P<0.05$) conjugated linoleic *c*-9, *t*-11 acid than did intramuscular tissue. The conjugated linoleic *c*-9, *t*-11 acid content of intramuscular tissue was greater ($P<0.05$) in the Forage Fed and <90 Day treatments than in the 50:50 Forage:Grain and Feedlot Finishing treatments. Alpha-linolenic acid content was greatest ($P<0.05$) in intramuscular tissue of Forage Fed bison than the other treatments. Total omega-3 fatty acid concentration was greater ($P<0.05$), in the intramuscular tissue of Forage Fed bison, followed by <90 Day and 50:50 Forage:Grain being similar ($P>0.05$) with Feedlot Finishing having the lowest ($P<0.05$) content. Eicosapentaenoic, docosapentaenoic, and docosahexaenoic acid were all found in the greatest ($P<0.05$) proportion in the Forage Fed, and least ($P<0.05$) in the Feedlot Finishing treatment.

The total omega-6 and arachidonic fatty acid content of intramuscular tissue was greater (*P*<0.05) in the Forage Fed and 50:50 Forage:Grain than in the <90 Day or Feedlot Finishing treatments. The omega-6 to omega-3 fatty acid ratio was greatest (*P*<0.05) for the 50:50 Forage:Grain followed by <90 Day with Feedlot Finishing being intermediate, and Forage Fed bison having the lowest (*P*<0.05) ratio.

Feedlot bison were compared to beef (*Bos taurus*) steers (n=4) and sheep wethers (*Ovis aries*) (n=3). Sheep had lower (*P*<0.05) saturated fatty acid content than did bison or beef in intramuscular tissue. Polyunsaturated fatty acid content of intramuscular tissue was greater (*P*<0.05) in bison than in beef or sheep. The ratio of polyunsaturated to saturated fatty acids was greater (*P*<0.05) for bison than for beef or sheep. The omega-6 to omega-3 fatty acid ratio was lower (*P*<0.05) for the bison than the beef, while sheep were intermediate (*P*<0.05).

Forage Fed bison compared to forage fed sheep wethers (n=3) showed that the ratio of polyunsaturated to saturated fatty acids was greater (*P*<0.05) in bison than sheep. The ratio of omega-6 to omega-3 fatty acids was similar (*P*>0.05) for both species.

Forage Fed bison yielded the greatest proportion of beneficial fatty acids amongst the bison treatments. Comparison of species under feedlot and forage finishing systems indicated bison to have a more desirable fatty acid profile than did beef or sheep finished under their respective systems.

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1.0. Introduction

Bison production represents a growing specialty market for ruminant meat production. As the industry grows, there will be more demand for information on how to feed bison for market and how the animals perform under different feeding strategies. Limited studies have been made into feeding practices and nutritional requirements of bison. Rutley and Hudson (2000) observed bison activities while grazing seeded pasture, noting seasonal shifts in metabolizable energy intake. Estimated maintenance requirements decreased in winter corresponding to decreasing nutrient values of forages. Both Anderson et al. (1996) and Church et al. (1999) have studied bison performance under feedlot settings, both noting seasonal influence on intake and weight gain. Anderson et al. (1996) noted slight changes in growth performance based on feed ingredients. Stanton et al. (1995) explored the effects of concentrate level in bison feedlot diets, noting large seasonal effects but also an improved feed efficiency when feeding 70% corn based diets as opposed to 30 or 50% concentrate. There is a need to further investigate finishing strategies and dietary ingredients on bison growth performance.

If bison meat products gain more acceptance, there will be increasing interest in the eating quality and nutritional value of the products. Comparison of bison to other domestic ruminants is resulting in a rethinking of conventional processing methods to improve meat quality (Janz et al. 2000). For example, bison meat tenderness was significantly improved by slowing the carcass cooling process post slaughter (Janz et al. 2000). There is limited nutritional quality information available regarding bison meat. Bison meat is generally regarded as being low in sodium as well as providing more than 20% of the daily requirement of vitamin B_{12}, phosphorus and zinc per 100 g fresh meat serving (Marchello and Driskell 2001). Initial investigations report meat from feedlot fed bison to be low in total fat, low in saturated fat, and high in protein, according to the

American Food and Drug Administration (Marchello et al. 1998, Marchello and Driskell 2001). Comparison of meat from forage to feedlot fed bison indicates forage fed to contain slightly less total fat (Marchello and Driskell 2001). Fresh meat cuts from both forage and feedlot fed bison contained less than 1g 100 g^{-1} saturated fat (Marchello and Driskell 2001). Comparisons of fatty acid profiles between forage and feedlot fed bison indicate forage fed bison to be lower in total fat, saturated fat and higher in total polyunsaturated fat (Rule et al. 2002). Comparisons of forage and feedlot fed beef to bison show total fat content to be similar between forage fed bison and beef, while the total fat content of feedlot fed beef was greater than that of feedlot fed bison (Rule et al. 2001). The palmitic acid content of forage and feedlot fed bison was also found to be lower than that of their beef counterparts (Rule et al. 2001).

The effect of individual fatty acids on human health is of considerable interest. Consumption of saturated fatty acids such as myristic and palmitic acid have been shown to increase low-density lipoprotein cholesterol, leading to increased risk of cardiovascular disease. Conjugated isomers of linoleic acid have been shown to exhibit anticarcinogenic and antiatherosclerosic effects, along with enhancing body immune function, and positive influences on body composition. The two fatty acids essential for mammalian development are linoleic, found primarily in cereals and oilseeds, and α-linolenic acid, found primarily in association with chloroplasts of green plants. Long chain polyunsaturated omega-6 fatty acids derived from linoleic acid, in particular arachidonic acid, are responsible for producing pro-inflammatory eicosanoids. The long chain polyunsaturated omega-3 fatty acids derived from α-linolenic acid, including eicosapentaenoic, docosapentaenoic, and docosahexaenoic acid, all demonstrate positive effects in human health. Eicosapentaenoic acid is the precursor of anti-inflammatory eicosanoids, and along with docosapentaenoic and docosahexaenoic acid, is involved in reducing the risk of cardiovascular disease. The optimal ratio of dietary omega-6 to omega-3 fatty acids is debatable but is generally considered to be 4:1. While linoleic acid is the predominant polyunsaturated fatty acid found in western diets (Simopoulos 2000), however its influence can be moderated by the actions of α-linolenic acid through competitive inhibition. The elongation/desaturation of linoleic and α-linolenic acid use the same enzyme pathways; however, omega-3 fatty acids are more competitive for the actions of the elongase/desaturase enzymes along with being more readily incorporated into the production of eicosanoids (Boissonneault 2000). The ratio of omega-6 to omega-3 fatty acids was found to be similar in forage fed bison and beef, both being half that of their feedlot counterparts (Rule et al. 2001). Duckett et al. (1993) noted a shift in diet from a primarily forage to concentrate based diet resulted a change in the fatty acid profile of fresh beef tissue, where the proportion of myristic and palmitic acid increased with time on concentrate diets. The limited information available for comparing forage to feedlot fed bison provide a starting point for further investigation into the effects of diet on tissue fatty acid profiles and their potential influence on human health.

Short-term concentrate feeding effects on beef have been shown to reduce the proportion of polyunsaturated, especially the omega-3, fatty acid content of beef tissues. Similar effects are expected with bison; however, the extent of the effects are largely speculative without further investigation. Different combinations of concentrate and forage are popular finishing practices amongst bison producers within Saskatchewan. The influence of concentrates on the fatty acid profile of bison tissue will be dependent on the amount and availability of forage. Further research into bison feeding strategies will provide producers with data to demonstrate the impact of management decisions on the health aspects of the lipid portion of bison meat products.

Within this thesis there is a review of literature regarding the status of the bison within western Canada, particularly within Saskatchewan; an overview of what is currently known about some of the more biologically functional fatty acids and the impact they have on human health; a review of factors shown to have an influence on the fatty acid profiles of ruminant tissues, making reference to studies experimenting into how to influence the fatty acid profiles through dietary means.

The objectives of research presented are:

1. To compare how western Canadian bison finishing programs influence the fatty acid composition of adipose tissues and muscle tissue.
2. To compare the fatty acid profiles of bison tissue to that of western Canadian steers and wethers under intensive feeding and forage finishing conditions.

2.1. Bison in North America

2.1.1. Origin of Bison in North America

The Great Plains of North America covers 15% of the continental land mass. This grassland ranges from southern Alberta to northern Texas; it begins at the Mississippi River and extends to the foothills of the Rockies, encompassing roughly 2,000,000 square kilometers of short to tall grass prairie (Lott, 2003). *Bison bison* have historically roamed the entire area, as well as venturing into mountain foothills and tundra regions (Reynolds et al. 1982). The number of bison that may have grazed the plains is difficult to determine due to exaggerated historical estimates of sightings and uncertain estimates about where and how far the great herds migrated. The North American bison population at the beginning of the 1870's was estimated to be about sixty million animals (SAF, 1998); Seton first proposed this widely accepted number in 1929 (Shaw, 1995). Seton based his approximation on the personal accounts of Colonel Richard I. Dodge, who noted the size of a bison herd on one of his expeditions along the Arkansas River in 1871 (Lott, 2002). Based on accounts by Col. Dodge, Seton concluded that the Great Plains could support about sixty million bison (Shaw, 1995). More recent calculations based on the carrying capacity of the land by McHugh in 1972 have re-estimated the probable bison population before the beginning of the 1870's at thirty million head (Isenberg, 2000).

The introduction of horses, guns and European livestock diseases in the early 1800's all contributed to a dwindling of the bison population. The 1870's marked the beginning of the end for the bison herds (Lott, 2002). The industrial revolution was beginning, and the commercial slaughter of the bison began once tanners learned to utilize buffalo hides for belting for steam engines. By the early 1880's the North American bison population was all but wiped out (Lott, 2002), and by 1889 there was no more than an estimated one-thousand bison left in the United States (Arthun and Holecheck, 1982).

Conservation efforts to preserve the last few remaining bison were made by individual private owners who recognized the value of the bison for its cultural symbolism and a reminder of frontier life. The first organization with the sole purpose of protecting the few remaining bison in the United States was the American Bison Society founded in December of 1905, and between 1920 and 1930 helped to establish a number of federal bison reserves (Dary, 1974). The last national bison census by the American Bison Society in 1933 reported that there were 21,701 bison in captivity and by 1940 the society had become less active in promoting the preservation of buffalo (Dary 1974). By 1954, the American Bison Society was no longer listed as a wildlife protection organization (Dary 1974). A 1972 survey revealed that there were 30,100 bison in the United States of America on various wildlife preserves or privately owned (Dary 1974). Through conservation efforts, the bison species was saved; however the true essence of the wild bison was limited due to the genetic bottleneck imposed on the species by the actions of man. Almost all bison that are under government or private management today can be genetically traced back to one of five populations under private management at the end of the 1880's (Schnabel et al. 2000).

2.1.2. Bison Industry Today

As a result of the successful conservation efforts in the last century, bison are no longer under the threat of extinction. Commercial production of bison in western Canada currently revolves around the sale of breeding stock, meat, and carcass by-products such as heads and hides or sales to hunt farms (Hawley 1986). Most privately managed bison are being raised for meat production (Schnabel et al. 2000).

Grazing is one of the most practical ways to use the vast expanses of native vegetation of the North American plains. Bison have proven their ability throughout history to survive in some of the harshest weather conditions found in North America (Christopherson et al. 1979). Trials to determine the ability of bison to handle cold stress have demonstrated their superiority over domestic cattle. By placing bison and beef calves in respirations chambers, Christopherson et al. (1979) was able to show that bison calves at six months of age were as tolerant to -30°C as seventeen month-old Hereford calves. One of the key advantages of bison is their ability to reduce their metabolic rate during cold periods, which corresponds to a time of seasonal low feed availability (Christopherson 1978). The bison's natural ability to forage under harsh conditions such as deep snow or poor quality forage has allowed them to thrive with minimal management (Rutley 1998). Longer rumen retention times and more extensive fermentation are key factors to bison's superiority on low quality feeds; however this advantage over domestic livestock is lost when presented with good quality forages (Richmond et al. 1977). The bison's suitability to prairie conditions makes them an ideal low management alternative to traditional domestic beef production. The mass of marginal land across the Great Plains area ensures there will always be a niche for bison. One of the current issues with bison production is whether to impose traditional beef management practices on bison or conform current management practices to take advantage of their unique abilities.

2.1.3. Current Industry Status

In 2000 there were 370 bison ranches operating in Saskatchewan (Saskatchewan Agriculture & Food, 2002). The most recent census of Saskatchewan bison herds was carried out in the fall of 2001 and estimated the total number of bison within the province to be 30,000 (Saskatchewan Agriculture & Food, 2002). In recent years the value of breeding stock has diminished, (Saskatchewan Agriculture & Food, 2001) and the need for alternative revenue sources has emerged. One way in which producers have been able to supplement farm income is the sale of mature animals to hunt farms. Unfortunately, there is not enough demand for trophy hunting to make hunt farms a viable solution for industry growth. The most popular method of generating additional income is through commercial bison production for meat. Bison that are not selected as breeding stock are grown out or finished to a desirable market weight.

2.1.4. Marketing of Bison in Saskatchewan

The market for bison meat as a leaner, healthier alternative to beef is currently in the development stages (Alberta Bison Commission, 2002). One of the obstacles to market growth is the lack of consumer exposure to bison products. Currently there is no central marketing board overseeing the production and promotion of bison meat within

Saskatchewan. The lack of a functional marketing organization leaves producers on their own to market their animals to the best of their ability. Another limitation to the rapid growth of the bison meat industry is the lack of a federally inspected slaughter facility in Saskatchewan. This limits the sale of bison products to in-province sales such that finished bison slaughtered in Saskatchewan can only be sold in Saskatchewan. Some producers have been successful in supplying local urban markets, such as restaurants with bison meat but many producers are limited to local farm gate sales which can be very sporadic. In order to make bison meat available to the North American market, bison must be slaughtered in a federally inspected facility, and for European export the facility must meet European Economic Community standards.

2.1.5. Human Health Benefits of Bison Meat Consumption

Since the introduction of bison meat products to the main stream consumer market, efforts have been made to address the nutritional qualities of the meat (Marchello et al. 1998). Physically, bison resembles domestic cattle (*Bos taurus*) in both size and metabolic functions. Although there is limited information available on the nutrient content of bison meat, preliminary analyses indicates bison to be very comparable to beef, albeit leaner. Protein and energy content of bison ribeye and chicken breasts were found to be similar (Marchello et al. 1989). On a wet weight basis, the protein content of beef and bison were similar, although the energy content of beef was higher due to the higher fat content of the muscle (Marchello et al. 1989). The majority of bison are grazed on forages for some period during the finishing process. This practice inevitably leads to an older, leaner carcass when compared to feedlot finished beef steers. Bison meat, whether finished on forage or grain (Table 2.1.), is considered to be both low in fat and cholesterol as classified by the American Food and Drug Administration (Marchello and Driskell 2001). According to the recommended dietary mineral allowances set by the American Food and Drug Administration, bison meat (Table 2.2.) is an excellent source of iron and is low in sodium (Marchello et al. 1998). Bison meat was also found to be an excellent source of vitamin B_{12}, phosphorus, and zinc (Marchello and Driskell 2001). Selenium content of bison meat finished exclusively on grass was four times that of feedlot finished bison (Marchello and Driskell 2001). The mineral content of muscle

varies with individual dietary mineral supplementation, making comparisons between trials difficult. Animals finished on pasture reflect the mineral content of the soil on which they were grazed. Fat and cholesterol content of muscle varied with how the animals were fed prior to market (Rule et al. 2001). Marchello et al. (2001) found grass-finished bison to be leaner than its feedlot counterpart. Fatty acid content varied with finishing program to a greater extent than variation between muscle sample sites (Marchello et al. 2001). The greatest variation between feedlot and grass finished bison was found in the fatty acid profile. Linoleic and α-linolenic acids are the primary fatty acids found in fresh forage, with their content decreasing as the forage matures.
Bison finished on forage tend to have a higher proportion of saturated fatty acids in the muscle tissue as a product of the extensive biohydrogenation of α-linolenic and linoleic acid within the rumen. However, the greater content of saturated fatty acids is off set by a greater proportion of polyunsaturated fatty acids. The advantage in the higher content of polyunsaturated fatty acids is further exemplified from the higher content of omega-3 fatty acids associated with increased intake of α-linolenic acid.

Table 2.1. Composition of raw separable lean tissue from grass and grain-finished bison

NUTRIENT	GRASS FINISHED	GRAIN FINISHED	NUTRITIONAL COMMENTS
Protein (%)	21.5	21.7	Excellent source of protein.
Moisture (%)	75.9	74.6	Typical of most meats.
Fat (%)	1.7	2.2	Low in fat. Low intakes associated with decreased incidence of heart disease & cancer. Diet should contain <30% of calories.
Saturated fat (% of fat)	47.4	42.5	
Monounsaturated fat (% of fat)	35.4	46.5	Low intakes associated with decreased incidence of heart disease & cancer. Higher proportion associated with decreased incidence of heart disease & cancer.
Oleic acid (% of fat)	34	42.7	Higher proportion perhaps associated with decreased incidence of heart disease.
Polyunsaturated fat (% of fat)	17.2	11	Higher proportion associated with decreased incidence of heart disease & cancer.
Linoleic acid (omega-6) (% of fat)	13.8	10.5	Recommended omega-6:omega-3 intake is 4-10:1.
Linolenic (omega-3) (% of fat)	3.4	0.5	
Cholesterol (mg $100g^{-1}$)	65	66	Lean Meat. Low intakes associated with decreased incidence of heart disease & cancer.
Food energy (kcal $100g^{-1}$)	133	141	Relatively low in calories.
Ash (%)	1.2	1.2	Reflective of total mineral content.

Source: Marchello et al. (1998), Marchello and Driskell (2001), taken from Smoke Signals, October 2001.

Table 2.2. Comparison of the vitamin and mineral content of raw separable lean tissue from grass and grain-finished bison

Mineral (mg $100g^{-1}$)	Grass Finished	Grain Finished	Nutritional comments	Mean % of Recommended Daily Value[z] Grass	Grain
Calcium (mg $100g^{-1}$)	5.5	4.9	Not a good source	<1	<1
Copper (µg $100g^{-1}$)	160	142	Some samples may contain over 10%, thus a good source	8	7
Iron (mg $100g^{-1}$)	2.8	2.9	Both are good sources	16	16
Magnesium (mg $100g^{-1}$)	25.8	24.2	Some samples may contain over 10%, thus a good source	6	6
Managese (µg $100g^{-1}$)	11.5	13.4	If use % lower estimated safe & adequate daily intake as is no daily value	<1	<1
Phosphorus (mg $100g^{-1}$)	181	198	Grass-finished is good source, while 18 grain finished is an excellent source	18	20
Zinc (mg $100g^{-1}$)	3.3	3.8	Both are excellent sources	22	25
Sodium (mg $100g^{-1}$)	44.7	52.2	Both are low in sodium	-	-
Potassium (mg $100g^{-1}$)	305	336	2000 mg is estimated minimum requirement	-	-
Selenium (µg $100g^{-1}$)	105	26	No daily requirement	191	47
Vitamin A (µg $100g^{-1}$)	-	0.8	Not a good source	-	-
β-carotene (mg $100g^{-1}$)	-	nd	Moderate intake levels may be associated with decreased heart disease & cancer	-	-
Vitamin C (mg $100g^{-1}$)	-	nd	Not a good source	-	<1
Thiamin (mg $100g^{-1}$)	-	0.043	Not a good source	-	3
Riboflavin (mg $100g^{-1}$)	-	0.94	Some samples may contain over 10%, thus a good source	-	6
Niacin (mg $100g^{-1}$)	-	1.011	Good source	-	10
Vitamin B6 (mg $100g^{-1}$)	-	0.24	Good source	-	12
Vitamin B12 (µg $100g^{-1}$)	-	2.565	Excellent source	-	43
Vitamin E (mg α-tocopherol)	-	0.048	Not a good source	-	<1

[z] Daily Value (given as a percentage) is an expression of recommended intake per serving that is utilized in the nutritional labelling (as Nutrition Facts) according to Food and Drug Administration regulations (1992).
Source: Marchello et al. (1998), Marchello and Driskell (2001), taken from Smoke Signals, October 2001.

2.2. Implications of Fatty Acids in Human Health

2.2.1. Essential Fatty Acids

Lipids, as a dietary component, have been shown to be more than just an energy source since the early 1920's (Simopoulos 1990). The simplest class of lipids is the straight chain hydrocarbon fatty acid molecules. Fatty acids are comprised of a carbon chain varying in length from four to over twenty-four carbon atoms (Hunt and Groff 1990). The negative charge of the carboxyl group positioned at one end lends to the polar nature of fatty acids. The number of carbons and the position of the double bonds within the chain determine the nomenclature of fatty acids. The most commonly reported nomenclature system, the International Union of Pure and Applied Chemists, is based on the carbon chain length, with a colon separating the chain length from the number of double bonds within the chain (O'Keefe 2002). The first carbon of the double bond, counted from the carboxyl end, denotes the position of the double bonds within the chain. The conformation of each double bond, be it *cis* or *trans* has an impact on the overall biological effect of the fatty acid (Appendix A). An alternate classification of fatty acids is the shorthand or omega system (ω), whereby fatty acids are grouped based on the distance the first double bond is from the methyl end (O'Keefe 2002). The two omega groups currently of significant interest are the omega-3 (ω-3) and omega-6 (ω-6) families, which are derived from α-linolenic and linoleic acid respectively. Medium chain fatty acids are considered to be those in the range of six to twelve carbons, while those with more than twelve carbons are often referred to as long chain fatty acids.

There are a number of fatty acids that research has shown to exhibit biological effects. These fatty acids can be traced to their original precursors, linoleic and α-linolenic acid. Linoleic and α-linolenic acid are the only fatty acids that are considered to be essential fatty acids, as they cannot be synthesized in mammals (Hwang 2002). Deficiencies in these essential fatty acids are manifested in clinical signs of retarded growth, reproduction and dermal symptoms (Chapkin 2000). From these two essential fatty acids, all other fatty acids of physiological importance can be derived via desaturation and elongation. Although it has been found that humans are not overly proficient at the elongase-desaturase activity necessary to produce adequate amounts of the longer chained polyunsaturated fatty acids, our diet can supply many of these functional fatty acids. Current research has found fatty acids of chain length C20:4, C20:5, C22:5, and C22:6, and conjugated isomers of C18:2, to influence biological activities within animals.

Some of the medium and long chain fatty acids found within animal tissue have been proven to have detrimental effects on human health. The most prominent detrimental effect of these medium and long chain fatty acids is their effect on cholesterol levels and the subsequent effects on the cardiovascular system. Palmitic (C16:0) is reported to have up to four times the cholesterolemic effect of either lauric (C12:0) or myristic (C14:0) acid (St. John et al. 1991). These three fatty acids have been implicated in raising the level of low-density lipoprotein (LDL) in blood, which is responsible for the transport of cholesterol from liver to tissues. Excess circulating cholesterol is deposited in the arteries forming arterial plaque, which causes the narrowing of arteries. Although these fatty acids are saturated, not all saturated fatty acids have detrimental effects. Stearic acid (C18:0) is not reported to have any effect on blood serum cholesterol (St. John et al. 1991). Fatty acids that contain at least one double bond in the *trans* configuration are also considered to be harmful to the cardiovascular system. Studies on the detrimental effects of *trans*-fatty acids have focused on the impact of partial hydrogenation of plant oils, in particular elaidic acid, and their links to coronary heart disease. Findings have shown that both *trans*-9 and *trans*-10 C18:1 are positively correlated to an increased risk of coronary heart disease, while no such link to *trans*vaccenic acid has been made (Bauman et al. 2004). One of the main byproducts of rumen biohydrogenation is *trans*vaccenic acid (C18:1 *t*-11), which can be found in significant amounts in ruminant tissues. The risk involved with consumption of naturally formed *trans* fats, in particular *trans*vaccenic acid, with respect to cardiovascular disease is considered minimal when compared to the risks associated with the *trans* fats arising from chemical hardening of oils (Scollan et al. 2001b; Bauman et al. 2004).

2.2.2. Conjugated Linoleic Acid

Fatty acid research has increased since the realization that certain conjugated isomers of the fatty acid C18:2, collectively referred to as conjugated linoleic acid (CLA), have implications in human health. In the early 1980's a group of scientists, led by Michael Pariza at the University of Wisconsin, isolated and identified a lipid component that was able to inhibit the growth of cancer cells. Since then, research has shown CLA to have a number of biological effects. Some areas where effects of CLA have been noted are immune function, atherosclerosis, weight gain, body composition and energy intake (Bauman et al. 1999). Conjugated linoleic acid is naturally produced in ruminant animals. The two main isomers are C18:2 *cis*-9, *trans*-11 and C18:2 *trans*-10, *cis*-12 (Fig 2.1.). These isomers are the intermediate result of bacterial biohydrogenation of linoleic acid to stearic acid (Qiu et al. 2004). Ruminants are also able to synthesize CLA from *trans*-11 octadecanoic acid via delta-9 desaturase during *de novo* synthesis.

2.2.2.1. Effect of Conjugated Linoleic Acid on Immune Functions

Conjugated linoleic acid may have an affect on energy partitioning within the body. When challenged by infection, CLA may increase the energy available to the immune system. During trials, CLA has been found to limit or nullify the effects of immune stimulation on growth performance (MacDonald 2000). After severe trauma, the body diverts energy away from immediately non-essential systems, such as the immune system, towards tissue repair. This, in turn leaves, the body susceptible to infection. Diets enriched with CLA have been shown to bolster the immune system during such periods of trauma (Pariza 1999). Cook and Pariza (1998) hypothesized that CLA indirectly affects the function/production of tumor necrosis factor-α (TNF-α) and interleukin-1 (IL-1). It is known that CLA affects eicosanoid synthesis, which regulates the production and function of TNF-α and IL-1 (Pariza 1999). The action of CLA

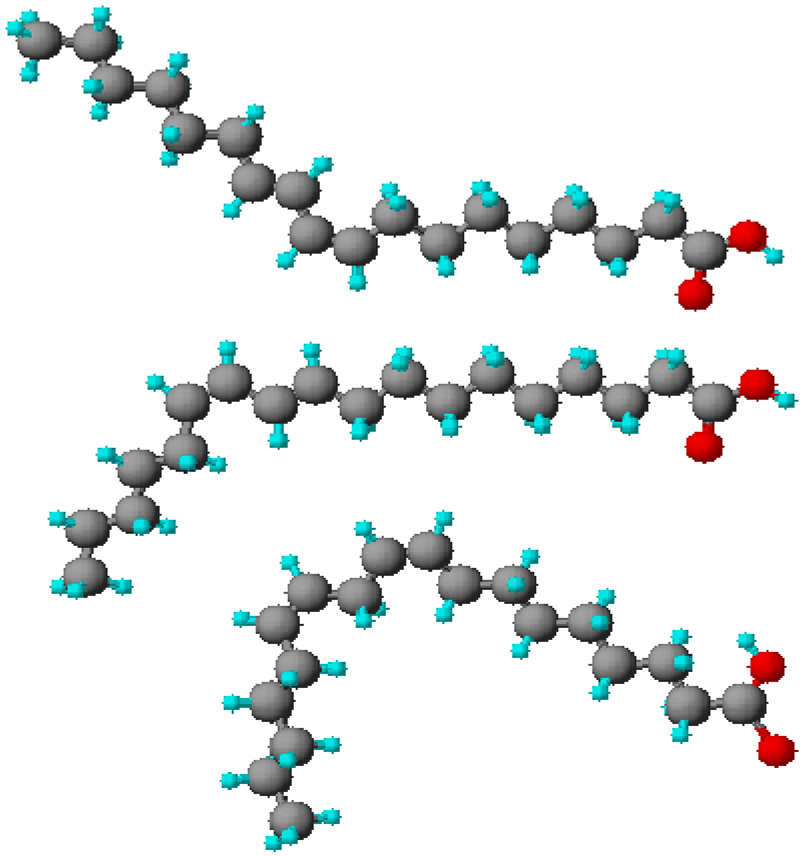

Figure 2.1. Structures of CLA *c*-9, *t*-11 (top), CLA *t*-10, *c*-12 (center), and linoleic acid, *c*-9, *c*-12-octadecadienoic acid (bottom). The molecules are aligned at their carboxyl end on the right to show how the double bond influences the structural shape of the molecule. (Image created with ACD Labs freeware ChemSketch ver. 8.0)

was found to reduce the arachidonic acid content of tissue, thereby reducing the availability of the eicosanoid precursor (MacDonald 2000). Yu et al. (2002) has shown that CLA exhibits anti-inflammatory effects by negatively regulating the expression of certain pro-inflammatory genes. By inducing the activity of peroxisome proliferators-activated receptor gamma (PPARγ) via CLA, there is a decrease in the production of pro-inflammatory products such as nitric oxide and TNF-α (Yu et al. 2002).

2.2.2.2. Conjugated Linoleic Acid and the Cardiovascular System

The inclusion of 0.5 g CLA day^{-1} in hypercholesterolemic diets (14% fat, 0.1% cholesterol) of rabbits reduced the total and low-density lipoprotein cholesterol levels in blood serum (Lee et al. 1994). The animals fed the CLA enhanced diets showed a reduced amount of LDL and triglycerides in the blood compared to controls. The aortas from the CLA fed animals also showed less atherosclerosis than those of the control group. Similar findings were found when using hamsters as the test subjects. The hamsters fed the CLA enhanced diets showed a decrease in plasma total cholesterol, non-high-density lipoprotein cholesterol and triglycerides without affecting the high-density lipoproteins (MacDonald 2000). Conjugated linoleic acid has been shown to have a beneficial effect by reducing atherosclerosis in animal models when included in the diet (Pariza 1999).

2.2.2.3. Effect of Conjugated Linoleic Acid on Body Composition

In studies where the *t*-10, *c*-12 isomer of CLA was included in the diet, changes to body composition included reduced body fat, increased body protein and ash, as well as enhanced body water content. Body composition is influenced by CLA in a dose dependent manner. Conjugated linoleic acid exhibited effects on both adipocytes and skeletal muscle cells (Pariza 1999). Addition of CLA to adipocytes showed reduced lipoprotein lipase (LPL) activity and increased lipolysis (Park et al. 1999). By hindering LPL activity, CLA is able to block the uptake of fatty acids by adipocytes, thereby preventing the growth of fat cells (Wang and Jones 2004). Other changes to body composition attributed to the *t*-10, *c*-12 isomer, such as increases in both body water and ash content, have also been noted by other researchers (Wang and Jones 2004).

A number of trials using mouse models have shown CLA to increase overall body protein content (Wang and Jones 2004). While overall body weight was not significantly different from control mice, 0.5% inclusion of CLA in the diet of mice caused a 57 and 60% lower body fat content and a 5 and 14% increase in lean body mass in male and female mice respectively (Hunter 2000). Long-term effects of CLA inclusion in the mouse diet indicated accretion of skeletal muscle when 0.5% CLA enhanced diets were fed (Park et al. 1999). Changes caused by CLA to body composition were still evident some eight weeks after CLA was withdrawn from the diet, and CLA levels had returned to levels exhibited by the control mice (Park et al. 1999). Protein accretion appears to precede body fat reduction in mouse trials (Park et al. 1999). Limited studies on humans have shown the consumption of 1 g CLA *t*-10, *c*-12 three times per day for three months resulted in an increase in lean body mass and a decrease in body fat content with no change in body weight (Hunter 2000).

2.2.2.4. Effect of Conjugated Linoleic Acid on Energy Intake

Conjugated linoleic acid has been found to improve feed efficiency in rat trials (Chin 1994). Numerous feeding trials have shown that rats, mice and chickens fed CLA enhanced diets tended to consume less feed for equivalent or greater weight gain compared to controls (MacDonald 2000). The reduced intakes of food associated with the intake of CLA are not considered to be significant enough to account for the observed reduction in fat deposition (Wang and Jones 2004). Along with reducing energy intake, CLA has been shown to increase energy expenditures by animals through increased metabolic rate (West et al. 2000). This increase in activity is in part responsible for the decreased adipose deposition observed in CLA-treated animals (Wang and Jones 2004). Increased energy expenditure has been linked to CLA's effects on uncoupling protein 2 (UCP2), a major uncoupling protein of white adipose tissue. The UCP2 activity is increased when influenced by CLA (Wang and Jones 2004). Increased activity of UCP2 caused by CLA would help to explain the increase in energy expenditure in animals fed CLA-rich diets.

2.2.3. Function of Omega-3 and Omega-6 Fatty Acids in the Diet

The optimal ratio of omega-6:omega-3 fatty acids is not fully understood, but recent estimates have placed the ratio for optimal growth in the range of 4:1 to 10:1 (Chapkin 2000). Western diets are estimated to be in the range of 10:1 to 15:1, with a large portion of lipids present either as saturated and *trans*-fats. In contrast, Japanese consumers consume seafood based diets containing a significant proportion of PUFA, with a ratio in the range of 4:1 to 5:1 (Chapkin 2000). Fish such as herring, mackerel, tuna or sardines contain relatively high proportions of eicosapentaenoic and docosahexaenoic acid, upwards of 80% of all PUFA's in the oil (Table 2.3). The reduction in omega-3 intake in modern diets is a result of decreasing consumption of seafood and the industrial production of animal feeds high in omega-6 fatty acids (Simopoulos 2000). The recommended intake of omega-6 fatty acids is approximately 4% of daily energy intake, while that for omega-3 fatty acids is approximately 0.75% of daily energy intake (Rule et al. 2002).

The actions of the omega-3 fatty acid family and the ratio of omega-6 to omega-3 fatty acids in the diet have been linked to numerous studies investigating blood platelet aggregation and cardiovascular disorders. Membrane fluidity, blood viscosity, receptor-agonist affinity, platelet-platelet and/or platelet-endothelial interactions, clotting factors and fibrinolysis are all affected by increased incorporation of omega-3 fatty acids into membrane phospholipids (Bruckner 2000).

Higher omega-6 to omega-3 ratios in skeletal muscle as a result of diet can inhibit insulin binding capacity, which results in an increase in the storage of adipose tissue (Ponnampalam et al. 2002). Diets high in omega-6 fatty acids have been shown to lead to hepatic and peripheral insulin resistance (Ponnampalam et al. 2002). Incidentally, inclusion of CLA in the diet has resulted in insulin resistance in some animal trials (Wang and Jones 2004). However, a number of studies have not shown any inhibitory effects of CLA on insulin activity/function, so no definitive conclusions can be made about adverse effects of CLA on insulin levels.

Table 2.3. Major marine oils of commerce, with weight percentages of saturated acids, 20:1+22:1, and 20:5+22:6

Oil	Saturated	20:1+22:1	20:5+22:6
	% Total Body Oils		
Body oils			
Herring (Atlantic)	19	35	14
Capelin	18	36	11
Redfish	21	36	9
Herring (Pacific)	34	10	7
Sand launce	24	27	17
Mackerel	27	38	15
Salmon (Pacific)	26	17	19
Sardine	30	8	24
Menhaden	32	2	20
Anchovy	30	3	26
Pilchard	28	5	26
Liver oils			
Cod (Atlantic)	21	13	24
Pollock (Alaska)	18	30	17
Squid (Pacific)	21	17	28
Other			
Salmon egg (Pacific)	?	?	?
Seal (Atlantic)	14	17	14

Ackman and Ratnayake *in* Omega-3 fatty acid in health and disease (1990).

2.2.3.1. Linoleic Derived Omega-6 Fatty Acids

Linoleic acid is the most predominant PUFA found in the Western diet (Simopoulos 1990), and is the precursor to the omega-6 fatty acid family. There has been an enormous increase in the consumption of omega-6 fatty acids as the consumption of processed vegetable oils has replaced the use of butterfats in food preparation. Vegetable oils from soybean, corn, and canola, all are higher in linoleic acid (Table 2.4), with a lesser amount of α-linolenic acid content (White 2000). Processing of vegetable oils converts the highly oxidizable omega-3 fatty acids, to a more stable monounsaturated form to increase shelf life of the product; however greater amounts of monounsaturated fatty acids having the *trans* configuration are also formed. Beef feedlot diets generally are high in linoleic acid content and generally result in an increase in the amount of saturated fats as well as increasing the concentration of omega-6 fatty acids at the expense of the omega-3 fatty acid family (Cordain et al. 2002). Through desaturation and elongation steps, linoleic acid gives rise to the omega-6 fatty acid groups, of which arachidonic acid is the most abundant twenty-carbon fatty acid found in terrestrial animals (Hwang 2000). Eicosapentaenoic acid is derived from α-linolenic acid and is the omega-3 counterpart to linoleic derived omega-6 fatty acids. Arachidonic (C20:4 omega-6) and eicosapentaenoic (C20:5 omega-3) acid are important precursors to eicosanoids (Fig 2.2.), which are involved in a number of physiological functions such as lowering blood pressure, diuresis, blood platelet aggregation, and inflammatory effects on the immune and nervous system (Hunt and Groff 1990). Eicosanoids derived from omega-6 fatty acids have the opposite metabolic properties compared to those derived from omega-3 fatty acids. The desaturation/elongation enzymes have a preference for omega-3 over omega-6 fatty acids (Chapkin 2000). An increase in the omega-3 levels in the diet, such as by increasing dietary content of α-linolenic acid, could be used to modify the amount of eicosanoids produced from eicosapentaenoic acid (C20:5 omega-3). Over-supplementation of arachidonic acid has been linked to over production of proinflammatory and proasthmatic eicosanoids in mice (Whelan et al. 1992). Eicosanoids derived from arachidonic acid are associated with a shift in the physiological state to one that is prothrombotic and proaggregatory leading to increased

Table 2.4. Fatty acid content of major edible vegetable oils[z]

	Palmitic	Stearic	Oleic	Linoleic	α-Linolenic
Canola	3.9	1.9	64.1	18.7	9.2
Corn	12.2	2.2	27.5	57.0	0.9
Linseed	4.8	4.7	19.9	15.9	52.7
Soybean	11.0	4.0	23.4	53.2	7.8
Sunflower	6.8	4.7	18.6	68.2	0.5

[z] Fatty acid composition expressed as mean average weight percent composition.

Adapted from White *in* Fatty acids in oilseeds (vegetable oils) *in* Fatty acids in foods and their health implications (2000).

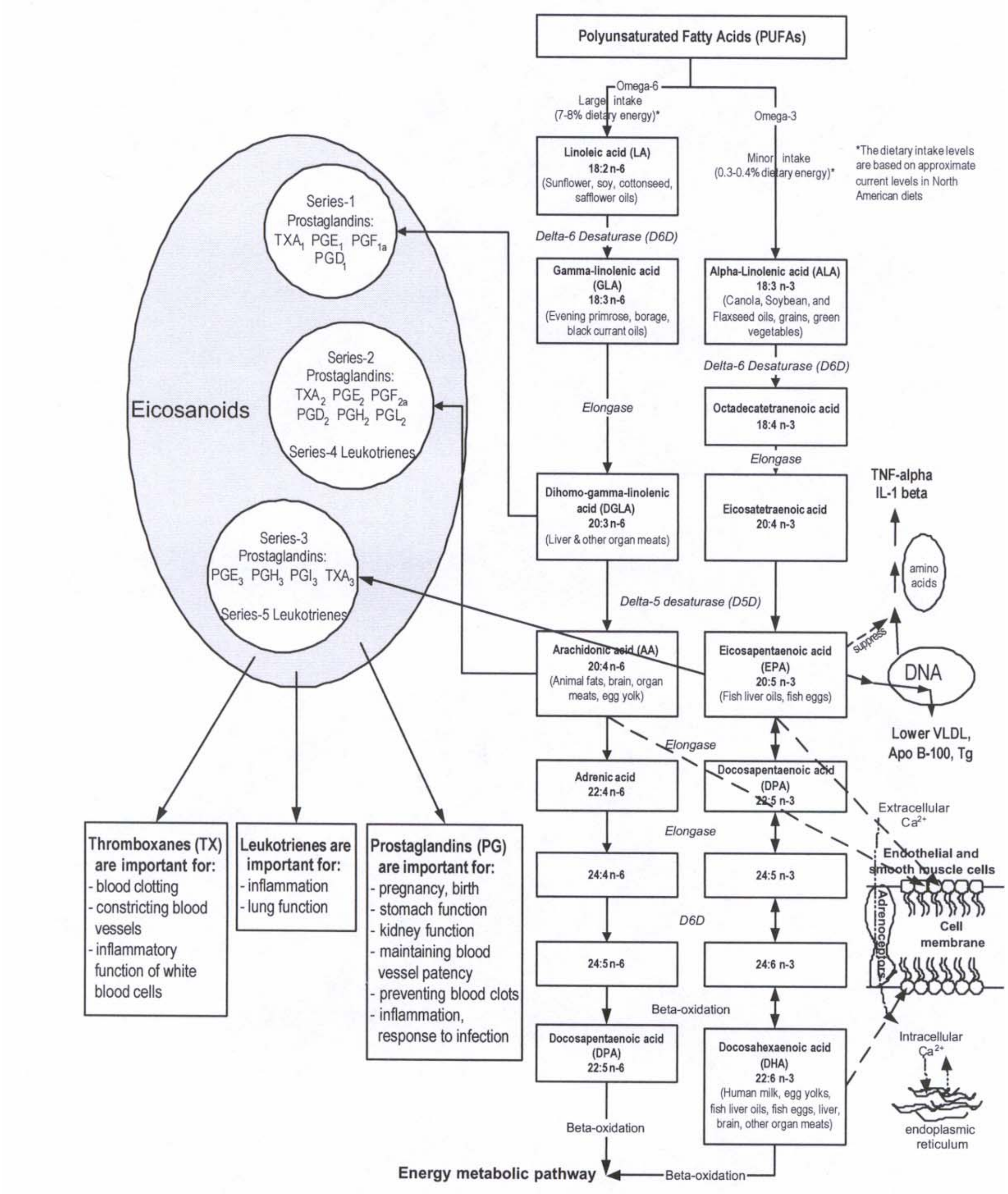

Figure 2.2. Function of eicosanoids produced from linoleic (omega-6) and α-linolenic (omega-3) precursors.
(Source: Agency for Healthcare Research and Quality 2005)

blood viscosity and vasoconstriction (Simopoulos 2000).

2.2.3.2. α-Linolenic Derived Omega-3 Fatty Acids

α-Linolenic acid is the major lipid found in the chloroplasts of green plants. α-Linolenic acid is the precursor to eicosapentaenoic, docosapentaenoic, and docosahexaenoic acid, all of which are important members of the omega-3 family of fatty acids (Appendix A). Research into docosapentaenoic acid focuses mainly on its purpose as a precursor to docosahexaenoic acid. Studies have shown that docosapentaenoic acid also has potent anti-atherogenic activity (Kanayasu-Toyoda et al. 1996), which would tend to reduce the risk of heart disease. In the study by Akiba et al. (2000), washed rabbit platelets were pretreated with eicosapentaenoic, docosapentaenoic, and docosahexaenoic acid and then exposed to coagulants to observe platelet aggregation. The results of the study determined that all three were dose dependent in their effectiveness at inhibiting platelet aggregation. It was determined that docosapentaenoic acid was the most effective at reducing platelet aggregation, and thus arterial blood clotting at all dose levels when exposed to collagen and arachidonic acid induced aggregation.

One of the most important fatty acids in young human development is docosahexaenoic acid. In mammals abundant docosahexaenoic acid deposits can be found in the cerebral cortex, retina, testis and sperm (Simopoulos 1990). Docosahexaenoic acid is required at high levels for optimal mental functions such as early learning and visual performance (Wright et al. 1998). Sufficient levels can be obtained from breast-feeding provided the mother is eating a nutritionally balanced diet (Wright et al. 1998). Deficiencies of docosahexaenoic acid during pre- and postnatal development have been linked to poor development of visual acuity and cognitive capabilities. Docosahexaenoic acid has been used to treat physiological disorders such as dementia and bipolar depression (Conquer et al. 2000).

Other functions of the longer chain omega-3 fatty acids include their effect on the cardiovascular system. It has been suggested that docosahexaenoic acid is more effective at reducing the risk of chronic heart disease than in eicosapentaenoic acid (McLennan et al. 1996). Although eicosapentaenoic acid and docosahexaenoic acid have been reported to have tumor suppressant activity, they must be fed at levels exceeding 10% of the diet, whereas CLA is able to elicit equivalent responses at levels as low as 0.1% of dietary energy intake (MacDonald 2000).

Although no definite conclusions can be drawn from our current understanding of the functions and interactions of PUFA's, indications drawn from research would suggest that an increase in dietary omega-3 content with a corresponding decrease in omega-6 content would be beneficial to human health (Chapkin 2000). This would necessitate an increased consumption of foods high in α-linolenic acid. The consumption of ruminant animals fed on pasture would provide CLA in the diet as well as being a source of the longer chain omega-3 fatty acids.

2.3.0. Recent Research into Factors Influencing the Fatty Acid Profile of Ruminant Products

2.3.1. Types of Lipids

Muscle lipid consists primarily of triglycerides and phospholipids. Triglycerides are the major component of all fat deposits and are relatively nonpolar. Triglycerides consist of three fatty acids, primarily saturated and monounsaturated fatty acids, connected by a glycerol backbone. Phospholipids are comprised of two fatty acids and a phosphate group connected by a glycerol backbone. The negative charge of the phosphate group gives the lipid its polar nature, leading to the formation of bimolecular sheets, thus their frequent association with membranes (Hunt and Groff 1990). Phospholipids generally contain higher amounts of longer chain polyunsaturated fatty acids (PUFA's) than triglycerides (Wood et al. 2003). The association of PUFA with phospholipids in the membrane layer aids in the fluidity of the membrane. A higher content of PUFA is present in muscle tissue relative to abdominal or subcutaneous adipose tissue sites. The specificity of the phospholipid acyl transferases preferentially puts PUFA's into phospholipids, while the acyl transferases for the triacylglycerol syntheses have a much broader specificity and, therefore, deposit fatty acids into triacylglycerols similar to proportions that they are found in the diet (R. Pegg, personal communication, Dept. of Applied Microbiology and Food Science, University of Saskatchewan, Saskatoon, SK). However, there are a number of other factors influencing the content of fatty acids in these fat deposits. Factors such as animal species, tissue site, diet, breed, sex, age and environment all affect fatty acid profile (Rhee 2000).

2.3.2. Factors Affecting Δ^9-desaturase Activity

Enzymatic desaturation of fatty acids removes two hydrogen atoms, creating a double bond between the carbons. The Δ denotes the position from the carboxyl end in which the double bond is inserted. The degree of saturation of depot fat varies with distance from the body core. It is well documented that the subcutaneous fat is more unsaturated than fat deposits around the kidney (Rhee 2000, Marmer et al. 1984; Bolte et al. 2002). While feeding a corn-based diet, the total amount of saturated fatty acids in subcutaneous tissue was found to be the lowest during winter months, (Link et al. 1970) while the highest levels were recorded during the spring and early summer. Seasonal effects on the fatty acid profile of tissues are most likely limited to subcutaneous adipose tissue where temperature influences will regulate desaturase activity (Tume 2004). The necessity to lower the melting point of subcutaneous adipose tissue maintains tissue fluidity, thereby facilitating other physiological functions. The actions of Δ^9-desaturase is primarily responsible for regulating the tissue fluidity during extreme temperature changes. Heat or cold acting in an inhibitory or stimulus capacity for desaturase enzymes has been postulated as the cause of the seasonal effect observed (Link et al. 1970).

Dietary factors can also have an effect on the desaturation process within tissues. Cyclopropenoic fatty acids, such as sterculic and malvalic acid, both found in cottonseed, have been shown to inhibit Δ^9-desaturase activity (Tume 2004). The effect of these inhibitors is to increase the proportion of saturated fatty acid in the tissue, resulting in a harder fat (Tume 2004). Inferences have been made that the higher the content of PUFA available from the diet, the more Δ^9-desaturase activity is inhibited in the tissue (Bolte et al. 2002). The depressive effect on the ruminal biohydrogenation of the PUFA increases with increasing carbon chain length and double bond number (Griswold et al. 2003), making fish oil a very effective inhibitor because of its eicosapentaenoic and docosahexaenoic content.

2.3.3. Conjugated Linoleic Acid Deposition

There is some conjugated linoleic acid (CLA) present in the lipids of plant material (Jehreis et al. 1997). However, animal products generally have a higher content with ruminant products being richer in CLA than those from monogastrics (Jiang et al. 1996). Dairy products tend to be the richest source, with CLA contents ranging from 2.5 to 8 mg g^{-1} lipid (Jehreis et al. 1997). Dairy products are the most abundant source of CLA but ruminant meat also contributes to daily intakes of CLA.

The CLA content of ruminant tissue is a result of either intermediates escaping biohydrogentaion in the rumen or endogenous production within the tissues. Very little natural CLA found in feedstuffs escapes biohydrogenation and is directly incorporated into the tissue. The conversion of *trans*vaccenic acid (18:1 *t*-11) to stearic acid appears to be the rate-limiting step during the biohydrogenation of linoleic acid and both α- and γ-linolenic acid within the rumen (Fig 2.3.).

An increase in the amount of linoleic acid has been shown to inhibit the biohydrogenation process of the microbes in an *in vitro* setting (Scollan et al. 2001), thereby slowing the conversion of *trans*vaccenic acid to stearic acid. Diets higher in unsaturated fats have the ability to overwhelm the saturating activities of the microbes (Bolte et al. 2002). Thus, a substantial amount of C18:1 *t*-11 escapes the rumen and is passed on to the rest of the digestive system (Fig 2.4.).

Within the rumen, a small amount of CLA is produced, primarily by the bacterial species *Butyrivibrio fibrisosolvens A38* (Harfoot and Hazlewood 1997), via the activity of the linoleate isomerase (EC 5.2.1.5) enzyme found in conjunction with the bacterial cell membrane (Bauman et al. 1999). Although the enzyme is able to form the *cis*-9, *trans*-11 conjugated isomer from the *cis*-9, 12 diene as found in linoleic, α-, and γ-linolenic acid (Bauman et al. 1999), only the conversion of linoleic acid to its conjugated isomer results in the formation of CLA within the rumen.

Ruminally-produced CLA is not the most significant source of CLA to be found in animal tissues (Qiu et al. 2004). Endogenous production of CLA will vary by tissue due to precursor availability and enzyme activity. Although there are a number of CLA configurations, only two have been found to be of biological significance. The most common CLA isomer is the C18:2 *c*-9, *t*-11 configuration. Growing ruminants have a large amount of Δ^9-desaturase in adipose tissue as indicated by mRNA abundance and enzyme activity (Bauman et al. 1999; Griinari et al. 2000). Whereas in lactating ruminants, CLA is primarily produced by the mammary gland as indicated by the Δ^9-desaturase activity and amount of CLA present in milk fat. Bauman et al. (2001) stated that 75% of CLA *c*-9, *t*-11 in milk fat originates from synthesis within the mammary glands. The desaturase index measures the Δ^9-desaturase activity by calculating the

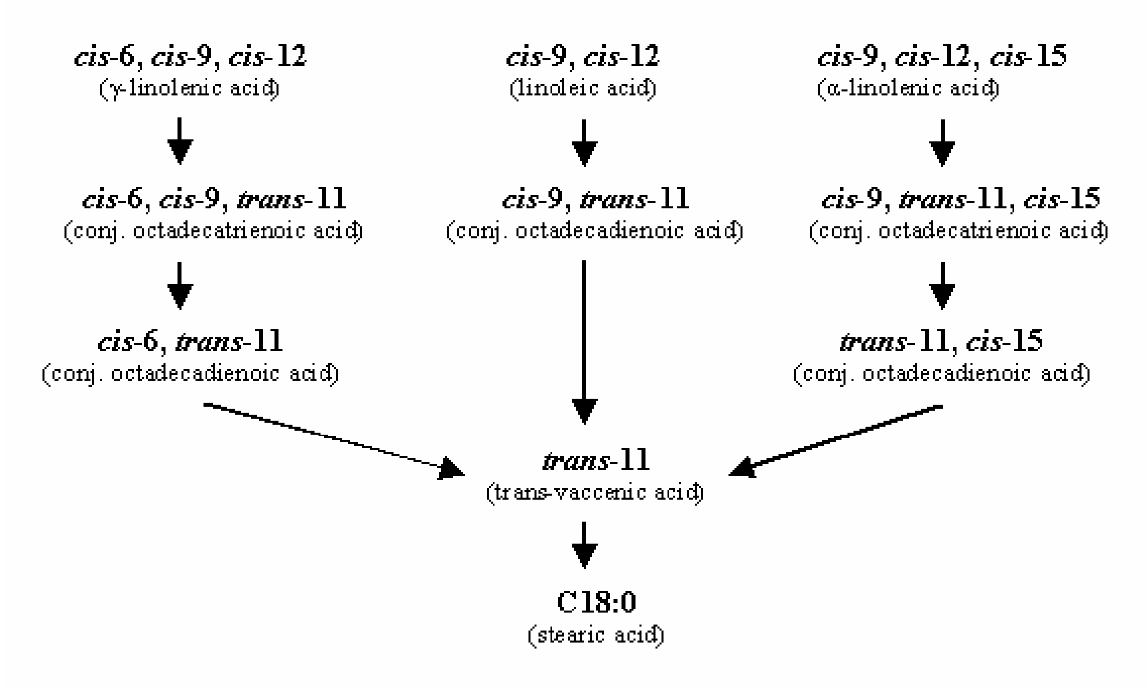

Figure. 2.3. Predominant pathways of ruminal biohydrogenation of unsaturated C18 fatty acids (Griinari and Bauman 1999).

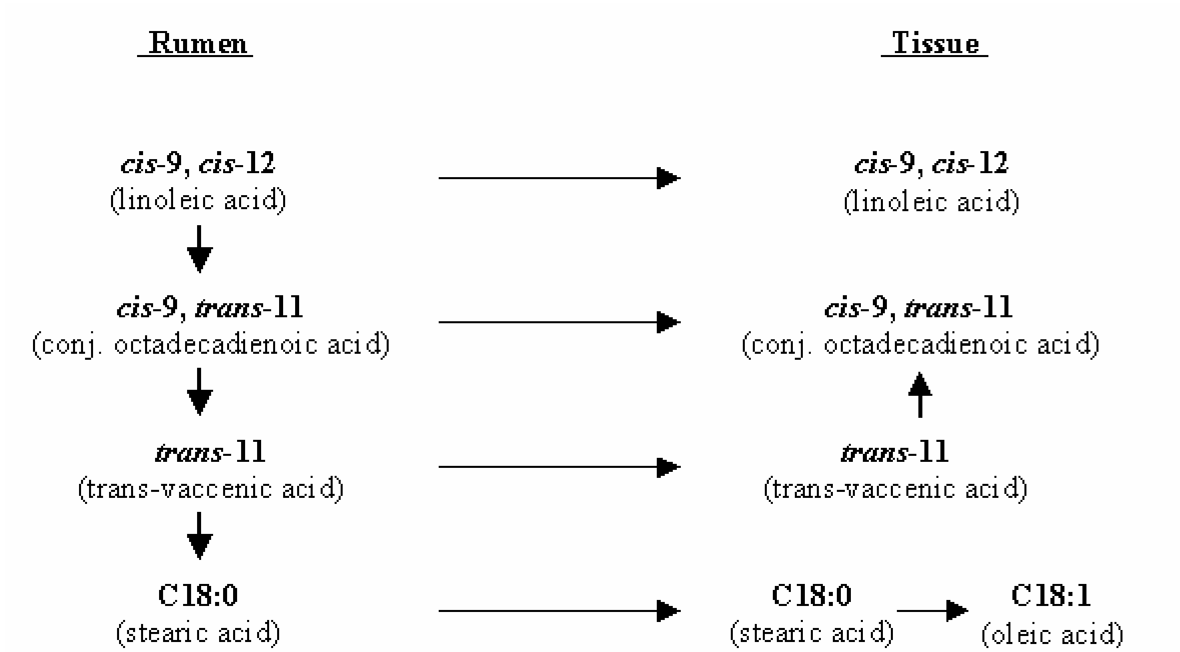

Figure. 2.4. Pathways of conjugated linoleic acid (CLA) biosynthesis (Griinari and Bauman 1999).

ratio between *trans*vaccenic acid and the *c*-9, *t*-11 isomer of CLA (Choi et al. 2000). Ratios between 14:1 *c*-9/14:0, 16:1 *c*-9/16:0, and 18:1 *c*-9/18:0 have all been proven to be valid methods of measuring Δ^9-desaturase activity in tissue, and estimated CLA production potential (Peterson et al. 2002).

Although the *c*-9, *t*-11 isomer is the most abundant isomer of CLA found in ruminant products, higher levels of CLA *t*-10, *c*-12 can be found in beef tissues than in milk fat (Mir et al. 2004). Forage-based diets yield the highest content of CLA in animal products as compared to diets consisting of high portions of concentrates (Bauman et al. 1999).

Diets high in forage content can be further manipulated by the addition of processed oilseeds rich in unsaturated fatty acids to increase the CLA content of the tissue (Aharoni et al. 2004). The inclusion of safflower or sunflower oil or seed appears to have the greatest effect on CLA content of ruminant muscle tissue (Mir et al. 2004). Sunflower oil fed at 6% of the diet has been shown to double the CLA content of muscle tissue from 10.5 mg to 19.5 mg $100g^{-1}$ (Mir et al. 2004).

Although diet has a substantial effect on the CLA content of milk, individual animal variation can be a significant factor when evaluating CLA production, regardless of diet (Peterson et al. 2000; Kelly et al. 1998). This individual animal variation is due largely to variation in rumen biohydrogenation along with Δ^9-desaturase activity of the mammary glands.

Amounts of CLA found in milk vary with the amount of CLA precursors present in the diet up to a plateau. During a ten-week study by AbuGhazaleh et al. (2004), CLA content in milk was increased by supplementing the diet with 2% of an extruded soybean meal plus 0.5% of a fish meal mixture. The CLA in the milk rose sharply in the first week, reaching a pinnacle by week 3 then decreasing slightly until week 5, after which it remained constant. The content of CLA in milk remained substantially above that of the control after supplementation began. The pattern observed for the concentration of CLA *c*-9, *t*-11 in milk was suggested by AbuGhazaleh et al. (2004) to be a result of microbial population adaptation to the CLA-stimulating diet.

An additional benefit from dietary supplementation with long chain polyunsaturated fatty acids is the resulting decrease in *de novo* synthesized fatty acids. Depression of short and medium chain length fatty acid synthesis through the supplementation of the lactating cow with polyunsaturated fatty acids would constitute an improvement to the fatty acid profile of milk, as it is the short and medium chain fatty acids that have proven to be hypercholesterolemic (AbuGhazaleh et al. 2004).

Seasonal effects have been shown to cause a shift in the amount of CLA present in animal products. A study by Thorsdottir et al. (2004) showed that milk collected from Nordic countries, which experience large seasonal variation, contained significantly greater amounts of CLA in summer months than in winter. This has been attributed to the time animals spend consuming fresh forage in the summer as opposed to dried or ensiled forage during the winter periods. This trend was also observed by Precht and Molkentin (2000) when comparing fat contents in relation to seasonal housing/feeding regimes. The highest concentrations of CLA in milk were found during the period between May and September, while the lowest levels occurred during March (MacDonald 2000). Precht and Molkentin (2000) concluded that higher proportions of CLA were evident in summer when cattle were grazing pasture. The lipid content of pasture grasses tends to be high in α-linolenic (50%) and linoleic (25%) acid (Precht and Molkentin 2000). Analysis of fresh perennial ryegrass (*Lolium perenni L.*) showed that 98% of extracted fat is esterified, with 2% being in the free fatty acid form, but when ensiled, esterified fat drops to 51% with the remaining 49% being comprised of free fatty acids (Elgersma et al. 2003). Most of the lipid in fresh forage is esterified, making it more stable while the fat found in grass silage was mostly (70%) in the free fatty acid form, making it more readily available to biohydrogenation (Elgersma et al. 2004).

The conjugated linoleic acid content of meat has been shown to vary by country, which is a reflection of beef finishing practices. Australia has some of the highest concentrations (1% of total fatty acids) while the USA has some of the lowest (0.3-0.5% of total fatty acids) (Griinari and Bauman 1999). This trend can be explained since most beef in Australia is finished on grass, while beef in the United States is finished on corn and corn silage diets. The finishing practices currently employed in North

America could be limiting the CLA available from animal tissue and products (Cook and Pariza 1998). By not exploiting the potential to increase the CLA available from ruminant tissue, the full health effects from consuming these products is not being realized.

2.3.4. Long Chain Polyunsaturated Fatty Acids and the Omega-6:Omega-3 Ratio

In North America, ruminants have traditionally been finished on diets consisting of concentrates and silage from corn or barley. Animals finished on forage are considered to be less desirable due to less overall fat content, increased proportion of unsaturated fats, and their fatty acid composition (Marmer et al. 1984; Marchello and Driskell 2001). The high content of linoleic acid found in cereal-based diets has led to an undesirably high omega-6 to omega-3 ratio in North American beef products (Wood et al. 2003). Omega-6 to omega-3 ratios of feedlot finished beef are in the range of 15 to 20 to 1, while those finished on forage are around 4 to 1. Around the world, corn and sorghum are the predominant grains utilized in cattle feeding/finishing programs (Cordain et al. 2002). Cordain et al. (2002) draws a direct link between the practice of finishing beef on high grain diets to the rise in saturated and monounsaturated fatty acid levels found in beef tissue. The excess energy from feed is stored as depot fat, both as intermuscular, and later in the finishing process, as intramuscular fat. Consequently, there is a dilution effect on the total PUFA’s present in the beef tissue. The nature of the lipid profile found in corn and sorghum, which both contain a relatively high ratio of omega-6 to omega-3 fatty acids, is responsible for the higher content of omega-6 to omega-3 fatty acids observed in the cattle tissue (Cordain et al. 2002).

Manipulation of the fatty acid profile of monogastric animals is easier because PUFAs can be incorporated directly from diet into tissue (Rhee 2000). The saturation activities of the ruminant microbial flora play a large part in determining what fatty acids are available for incorporation into tissues. Microbial biohydrogenation of eicosapentaenoic and docosahexaenoic acid *in vitro* has been shown not to occur to any significant level (Scollan et al. 2001b). This incomplete biohydrogenation process allows for these fatty acids to escape the rumen, making these unsaturated fats available for incorporation into muscle and adipose tissue. The ability of microbes to biohydrogenate long chain fatty acids found in fish oil tends to be dose dependant as observed by *in vitro* trials (Scollan et al. 2001). Fish oil was found to be more inhibitory to the biohydrogenation process than α-linolenic acid, allowing for more unsaturated fatty acids to escape the rumen (Scollan et al. 2001b).

Studies on inclusion of long chain PUFA's in the diets of ruminants indicate that there is only limited rumen microbial modification of omega-3 fatty acids of carbon chain length 20 or 22 (Ponnampalam et al. 2001; Scollan et al. 2001). Supplementation of a basal forage diet consisting of oaten and lucerne chaff with fish oil resulted in increases in the eicosapentaenoic (36.2 mg 100 g^{-1} fresh meat) and docosahexaenoic (18.1 mg 100 g^{-1} fresh meat) acid content of lamb meat compared to the control diet (13.8 and 5.5 mg 100 g^{-1} fresh meat, respectively) (Ponnampalam et al. 2001b). Similar results were observed comparing lupin seed to fishmeal supplementation. During this trial Ponnampalam et al. (2002) observed that sheep supplemented with fishmeal had a higher long chain omega-3 fatty acid content in the ribeye than sheep fed the lupin diet, which contain significantly less omega-3 fatty acids. By taking advantage of the ability to overwhelm the biohydrogenation activity of the microbes, there is the potential to increase the amount of PUFAs available for absorption by the animal. By incorporating more α-linolenic acid into ruminant diets, there is the potential to increase the amount of omega-3 PUFAs such as eicosapentaenoic and docosahexaenoic acid in the tissue via *de novo* synthesis (Scollan et al. 2001b).

Although trials have been successfully conducted to increase the amount of omega-3 fatty acids in ruminant meat by feeding fish meal, an undesirable off-flavour in the meat was detected. This is a result of incorporation of the fish oils into the ruminant meat (Mandell et al. 1998). Comparisons of eicosapentaenoic and docosapentaenoic acid levels in meat from animals fed either forage based or grain based diets supplemented with fish meal indicate that a higher concentration of eicosapentaenoic and docosapentaenoic can be reached by finishing animals on fresh forage diets (Mandell et al. 1998). However, as with the fishmeal diets, forage finished beef has been associated with off-flavours in the fat. This is due to the nature and composition of the fat. The higher the proportion of PUFA fed in the diet, the more that escapes biohydrogenation and is absorbed into the tissue. The extent to which the PUFA is unsaturated is positively correlated to its susceptibility to oxidation. The higher the PUFA content in the tissue and the degree of unsaturation, the greater the rate of autoxidation, resulting in a stronger off-flavor of the tissue (Larick et al. 1989).

The rancid/off flavour usually associated with forage fed animals is attributed to the increased content of PUFA within tissues and the highly susceptible nature of long-chained PUFA to oxidation. One of the chief culprits contributing to the "gamey" flavour experienced in meat from forage fed animals is the content of α-linolenic acid (McNiven et al. 2004). Contrary to previous findings, there was no increase in the oxidized flavour of lamb fed treatments enriched with various sources of PUFAs including fish oil (Ponnampalam et al. 2001b). The presence of higher levels of anti-oxidants, particularly vitamin E, found naturally in green leaves and grass would help to alleviate the problem of auto-oxidation.

2.3.5. The Effect of Forage Based Diets on Tissue Content of Omega-3 Fatty Acids

Trials by French et al. (2000) compared the effects of either a high forage or high concentrate diet on the fatty acid profiles of intramuscular fat in Limousin steers. Diets were balanced to maintain similar carcass gains to avoid confounding ration type and amount of carcass fat on fatty acid profile (French et al. 2000). Not surprisingly, the animals finished on the primarily forage diets contained higher levels of CLA and α-linolenic acid in the tissue, along with an overall increase in the PUFA content of the tissue. A reduction in the amount of unsaturated precursors would limit the animals ability to produce CLA in the tissue and milk (Thorsdottir et al. 2004; Jahreis et al. 1997).

French et al. (2000) illustrated that there was a linear decrease in the amount of saturated fatty acids (SFA) in tissue as concentrate levels decreased from 88% DM to 0%. The ratio of PUFA:SFA increased as the proportion of forage in the ration increased. In the animal tissue, a linear decrease in the omega-6 to omega-3 ratio was observed as forage content, containing α-linolenic acid, was increased (French et al. 2000).

Pastures and forages generally are low in C18:1 and C18:2 fatty acids and relatively high in α-linolenic acid, while the reverse is true of concentrate based diets

(Mandell et al. 1998). High concentrate diets result in an increase in body fat due to *de novo* synthesis of saturated fatty acids, but a decrease in milk fat production. High concentrate diets are normally low in total fat, in particular omega-3 fatty acids; and are usually fed during periods when fresh forage is not available (Precht and Molentin 2000). Lipids found in forages are in the glycolipid from and generally contain a large proportion of α-linolenic acid (Doreau and Ferlay 1994). Grasses are found to contain more fatty acids than legumes at any stage of growth (Loor et al. 2003). Greater amounts of α-linolenic acid was found in orchard grass compared to red clover (Loor et al. 2003), while red clover was higher in linoleic and oleic acid content (Table 2.5).

Ruminants finished on grain and dried or ensiled forage have been shown to contain less CLA in their tissues than ruminants finished on pasture (Cook and Pariza 1998). During the normal drying of forage, the α-linolenic content decreases and the palmitic acid increases (Dhiman et al. 1999). However, feeding alfalfa silage vs. a high moisture corn diet has been shown to significantly increase the proportion of α-linolenic acid in muscle tissue (Mandell et al. 1998). Differences in fatty acid profiles of muscle tissue can be attributed to the fatty acids available in the diet. Generally, glycerides found in seeds tend to be high in linoleic acid, while the predominant acid found in forages is α-linolenic acid (Itoh et al. 1999). Griswold et al. (2003) indicated that an increased forage content in the diet leads to an increased proportion of α-linolenic acid in muscle tissue.

The effect of forage source on the fatty acid composition of ruminant meat is variable. Using finishing lambs as a test model, Fraser et al. (2004) showed that legumes increased the content of α-linolenic and linoleic acid within the muscle, as well as increasing the PUFA to SFA ratio. The overall fat content of the meat was not different between forage sources. The differences between the biologically functional fatty acids, (CLA, eicosapentaenoic, docosapentaenoic, docosahexaenoic), also was not significant. However, feeding perennial ryegrass resulted in a statistically significant decrease in the omega-6 to omega-3 ratio relative to feeding red clover and lucerne legumes (Fraser et al. 2004).

Table 2.5. Content of 18-carbon fatty acids (FA) of typical feedstuffs

	FA content (g 100 g^{-1} FA)		
Feedstuff	Oleic	Linoleic	α-Linolenic
Dehydrated alfalfa[z]	6.5	18.4	39.0
Perennial ryegrass[z]	2.2	14.6	68.2
Pasture grasses[z]	3.4	13.2	61.3
Maize[z]	30.9	47.8	2.3
Barley[z]	20.5	43.3	4.3
Oats[y]	38.1	34.9	2.1
Canola oil[y]	61.0	21.0	11.0
Flaxseed oil[y]	16.0	18.0	57.0
Soybean oil[z]	22.5	50.8	6.8
Sunflower oil[y]	16.0	77.0	1.0

[z] Adapted from Beaulieu (2000).
[y] Adapted from Canola Council of Canada (2005)

Lee et al. (2003) indicated an increased flow of linoleic and α-linolenic acid from the rumen of steers fed white or red clover silage compared to perennial ryegrass silage. Once the effect of the clover on DM intake was accounted for, there was still a greater flow of linoleic and α-linolenic acid, with reduced flow of stearic acid to the duodenum. Reduced biohydrogenation activity found when the clover silages was fed was attributed to increased passage rate in the rumen of the white clover (Lee et al. 2003). The rumen dry matter turnover time of red clover silage was similar to ryegrass silage. Lee et al. (2003) postulated the reduced biohydrogenation activity was caused by chemical interference by polyphenol oxidase in the red clover, allowing more PUFA's to escape the rumen.

The use of forage in the diet has proven to be considerably more effective in raising the PUFA content, in particular the CLA content, of ruminant muscle tissue than the use of oil or oilseeds (Griswold et al. 2003).

2.3.6. Inhibition of Rumen Biohydrogenation

In order to increase the amount of PUFAs in ruminant tissues, more PUFA must escape the rumen biohydrogenation process. The rate of lipolysis in the rumen can be decreased with antibiotics (Scollan et al. 2001) or a reduction in pH (Dhiman 1999; Loor et al. 2003). Both methods would allow more triglycerides to escape the rumen, thereby avoiding biohydrogenation. Diets high in oil are also detrimental to fiber-digesting bacteria, which are responsible for the majority of the biohydrogenation of the unsaturated fatty acids (Griswold et al. 2003). From the study of Jiang et al. (1996), CLA production can be increased by restriction feeding a 65:35 (% DM), compared to a 50:50 (% DM) concentrate:forage diet. The pathway proposed would be that a decrease in pH from the high concentrate diet would reduce the number of biohydrogenating bacteria thus allowing more *trans*vaccenic acid to escape the rumen and allowing for greater incorporation into the tissue and further desaturation into CLA.

Efforts to reduce the biohydrogenation efficiency in the rumen have included feeding nitrogen deficient diets to alter the microbial population, and feeding processed feeds to alter the kinetics of fermentation and increase particulate passage rate (Lee et al. 2003). Gerson et al. (1988) showed that lipolysis and hydrogenation of lipids in larger feed particles was faster than that of smaller particles based on bacterial population density of the particles.

Alternative methods of increasing the amount of PUFA bypassing the rumen include the use of calcium salts, or fatty acid acyl amides and encapsulation of lipid in a formaldehyde treated protein matrix (Lee et al. 2003). Adipose tissue levels of CLA have been increased by the inclusion of CLA in the form of rumen-protected CLA salts. These salts are able to escape biohydrogenation and become incorporated into the tissues. By protecting the CLA in the rumen, biohydrogenation can be reduced from 70 to 30% (Gillies et al. 2004).

2.3.7 Minor Effects on Fatty Acid Profiles

Feed processing will change the fermentation dynamics of the diet. Reduced particle size will increase fermentation rate as a result of increased microbial density on the feed particle (Gerson et al. 1988). Increased fermentation rate can increase passage rate allowing some lipids to escape biohydrogenation. Processing of oilseeds by either extrusion or grinding for inclusion in the ruminant diet as a protein source can also affect the fatty acid profile of the animal. Rule et al. (1994) compared to the effect of processed and unprocessed canola and soybean on the fatty acid profile of the carcass. Extruded canola produced the lowest levels of myristic and palmitic acid along with the highest levels of linoleic acid in the muscle of steers (Rule et al. 1994). Rule et al. (1994) was not able to explain the differences observed between bulls and steers fed the same diet. Extrusion of whole canola seed resulted in more lipid bypassing the rumen allowing for greater absorption in the small intestine (Rule et al. 1994). High oil safflower seed has been shown to affect the fatty acid profile of ruminant tissue. In the feeding trial by Bolte et al. (2002), lambs were fed either high oleate (14.7% DM of diet) or linoleate (16.6% DM of diet) safflower seed to observe the effects of seed type on carcass composition. Seed high in linoleate increased the CLA content of the lamb tissue compared to the oleate or control diets. Differences between the lamb tissue samples were suggested to be a result of differences in Δ^9-desaturase activity. Incorporation of C18 fatty acids into tissues was linked to the higher dietary content of oleate and linoleate compared to the control animals (Bolte et al. 2002). Similar proportional shifts in the amount of C18 and longer fatty acids compared to those of *de novo* synthesis have been observed in other ruminant studies using canola seed, which is higher in linoleate.

The fatty acid composition of adipose tissue of beef animals changes with age. Link et al. (1970b) found that steers and heifers fed identical diets showed a reduction in the proportion of phospholipids within the muscle tissue as the animals aged and gained weight. Their conclusion was that the amounts of PUFAs present in the phospholipid layer are unchanged with age, but as an animal reaches maturity and begins to deposit significant amounts of marbling in the form of triglycerides, a dilution effect occurs. Similar results were found by Itoh et al. (1999), who compared steers fed on annual or perennial pasture or fed grain. Although age is known to have an effect on the fatty acid composition of the carcass, the interaction between age and fatty acid composition is minor compared to the affect of diet on fatty acid composition. Most animals are slaughtered at a relatively constant age as a result of the uniform feeding practices found in feedlot settings. Changes observed by Huerta-Leidenz et al. (1996) focused on the increase in stearic acid and decline in palmitic acid after weaning. Huerta-Leidenz et al. (1996) hypothesized that the observed changes, which have been observed or unnoticed in similar studies, might be due to an increase in the elongase activity in the adipose tissue. Breed differences played an equivalent if not greater effect on fatty acid composition than age (Huerta-Leidenz et al. 1996).

Link et al. (1970) found that the seasonal effects on fatty acid composition were greater than the effects associated with the age of the animal. As the animals aged, an increase in the amount of PUFA was observed in the ribeye tissue (Link et al. 1970b). The concentration of monounsaturated fatty acids has been shown to increase with the age of the animal as a trade off with the level of saturated fatty acids (Rule et al. 2002).

The time period for the greatest amount of intramuscular fat deposition in cattle is between 84 and 112 days when fed a high concentrate diet (Griswold et al. 2003). Short term feeding (6 weeks) with soybean oil at either 4 or 8% of DM was sufficient to alter the fatty acid profile of muscle tissue (Griswold et al. 2003). Conjugated linoleic acid content of the meat was enhanced with the addition of soybean oil, although an increase in the forage proportion of the diet seemed to have a greater effect (Griswold et al. 2003). The effect of short-term concentrate feeding was explored in an effort to improve the consumer's impression of meat quality. Forage finishing resulted in an increased content of carotenoids in the adipose tissue. These carotenoids caused a yellow appearance within the adipose tissue. There have been indications that as the fat becomes yellower the amount of *cis*-monounsaturated fatty acids increases and that of saturated and *trans*-monounsaturated fats decreases (Knight and Death 1997). In an effort to change the colour appearance, trials have been conducted where animals were switched to high grain diets, which are low in carotenoids, for a brief period at the end of the finishing phase. Successful colour changes have been reported by feeding for as few as sixty days (Forest 1981; Strachan et al. 1993 as cited by Morris et al. 1997), but there have been an equivalent number of trials where sixty days of concentrate was insufficient to change fat colour (Yang et al. 1993; Knight et al. 1996 as cited by Morris et al. 1997). Morris et al. (1997) found that feeding a high concentrate diet for thirty days to be insufficient to affect fat colour in finished beef steers

2.3.8. Comparing Cattle Research to Bison Studies

Assumptions that grass finished beef would be similar to meat from wild ruminants can be made, however there are exceptions. Although both are relatively low in saturated fats, grass fed domestic cattle have half to one-third the total polyunsaturated fatty acid content, and half to one-third the total omega-3 polyunsaturated fatty acid content of wild ruminants (Cordain et al. 2002). However, grain fed beef contains two to three times more total saturated fatty acids and only a third to a quarter of the total omega-3 polyunsaturated fatty acids than does a typical wild ruminant (Cordain et al. 2002) (Table 2.6).

Research into the fatty acid profile of wild ruminants may provide important clues to the composition and range of dietary fats to which humans are genetically adapted (Cordain et al. 2002). The changes in how ruminants have been finished over time and the observed links to human health will further our understanding of the implications of fatty acid intake on health. Simopoulus (2000) pointed to the shift in feeding practices from extensive grazing of ruminants to the more industrial production

Table 2.6. Comparison of muscle tissue lipid concentrations (mg fatty acid sample) in elk, mule deer, pronghorn antelope, pasture, and grain-fed cattl

Fatty acid	Elk	Deer	Antelope	Pasture-fed steer
SAT[z]	610	989	895	910
MUFA[y]	507	612	610	793
PUFA[x]	625	746	754	262
n-3 PUFA	178	225	216	61
n-6 PUFA	448	524	536	138
18:2 n-6	286	352	336	86
18:3 n-3	58	99	87	24
Long chain PUFA	281	295	331	152

[z] SAT, total saturated fatty acids
[y] MUFA, monounsaturated fatty acids
[x] PUFA, polyunsaturated fatty acids
Source: Cordain et al. (2002)

of animals being fed concentrate diets rich in omega-6 fatty acids (Fig 2.5.) to the rising incidence of many of the diseases afflicting Western nations (Table 2.7).

Comparisons between domestic cattle and wild ruminants show a higher proportion of PUFAs in the tissue of wild ruminants (Cordain et al. 2002). This would be indicative of a diet higher in unsaturated fatty acids typically found on pasture forage. As stated earlier, muscle lipid contains triglycerides and phospholipids. Since the phospholipid content is relatively constant, it is the triglyceride concentration, which has the greatest affect on the fatty acid profile of a given tissue. As the domestic ruminant nears the end of its high-energy finishing period, more triglycerides are incorporated into the muscle tissue. With more triglycerides infiltrating the muscle tissue, the fatty acid profile of the tissue changes to reflect that of the newly incorporated triglycerides. This change in concentration would account for the differences observed between wild ruminants, which do not generally go through a high energy finishing period like that of domestic cattle. Much of the triglyceride accumulation in domestic meat can be attributed to the appearance of interfascicular adipocytes, better known as marbling (Cordain et al. 2002). Analyses of the fatty acid profile of interfascicular fat and that of subcutaneous fat from grain-fed domestic cattle are very similar (Sweeten et al. 1990). Therefore, as the amount of marbling increases, the more meat tissue will resemble that of the subcutaneous fat layer.

When comparing *Bison bison, Bos taurus* and *Bos indicus* on the same corn based diet, bison were found to have the highest content of PUFA in *longissimus dorsi* tissue samples (Larick et al. 1989). These findings are suggested to be a result of genetic differences between bison and beef and differences in absorption of endogenously produced fatty acids. Different levels of finish may have confounded results, as all animals were slaughtered at roughly eighteen months of age.

The crude fat percentage of meat samples from feedlot finished bison varied by carcass region (Marchello et al. 1998), with top round containing 1.6% and the ribeye and sirloin containing 2.4% fat. Marchello and Driskell (2001) found that variation in the fatty acid profile amongst meat cuts in bison was minimal when comparing within a treatment group. However, it was noted that grass finished bison averaged a slightly lower percentage of fat per cut when compared to an equivalent cut from the feedlot

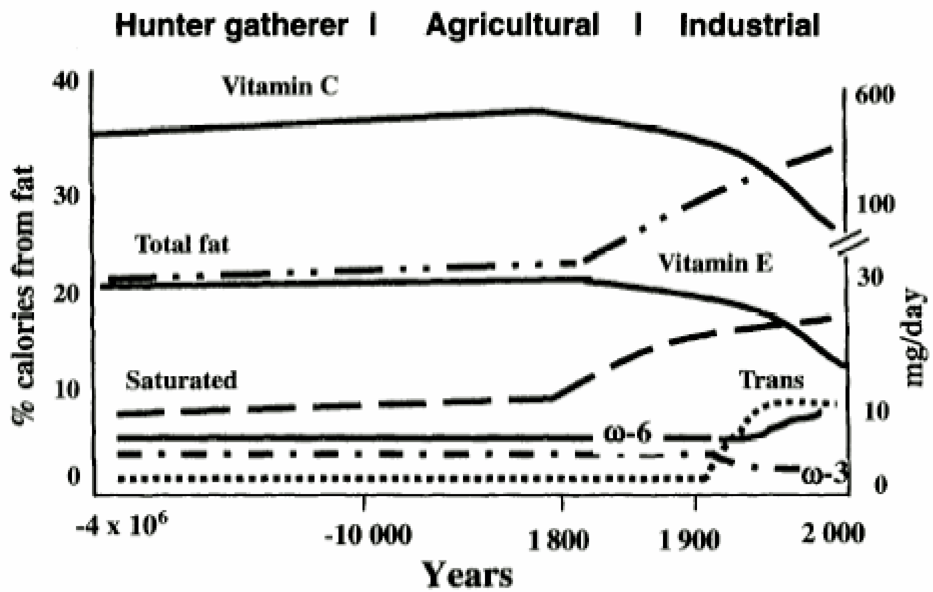

Figure 2.5. Hypothetical scheme of fat and fatty acid (ω-3, ω-6, *trans*, and total) intakes (as % of calories from fat) and intake of vitamins E and C (mg d^{-1}). Data was extrapolated from cross-sectional analyses of contemporary hunter-gatherer populations and from longitudinal observations and their putative changes during the preceding 100 years (Source: Simopoulos 2000).

Table 2.7. Ethnic differences in fatty acid concentrations in thrombocyte phospholipids and percentage of all deaths from cadiovascular disease[z]

	European and United States	Japan	Greenland Eskimos
		%	
Arachidonic acid (20:4n-6)	26	21	8.3
Eicosapentaenoic acid (20:5n-3)	0.5	1.6	8.0
n-6:n-3	50	12	1
Mortality from cardiovascular diesease	45	12	7

[z] Simopoulos (2000)

finished bison. In that study, meat samples from the ribeye (*longissimus dorsi*), top sirloin (*gluteus medius*), top round (*semimembranosus*) and shoulder clod (*triceps brachii*) were analyzed for a range of fatty acids. The variation of fatty acids between finishing techniques was significant. Bison finished on pasture contained more saturated and polyunsaturated, and less monounsaturated fatty acids, than the feedlot bison (Marchello and Driskell 2001).

Comparisons between range bison, beef and their feedlot counterparts by Rule et al. (2002) showed trends similar to the findings of Marchello and Driskell (2001). Pasture fed ruminants contained higher levels of α-linolenic acid in their tissues, while the feedlot ruminants contained higher levels of linoleic acid. This is a reflection of the lipid source found in the diets. Subsequently, range animal tissues contained more omega-3 fatty acids, thus decreasing the omega-6 to omega-3 ratio of the tissues closer to a 2 to 1 ratio (Rule et al. 2002). The elongated PUFA products of linoleic and α-linolenic acid were found in higher concentrations in feedlot and range fed animals, respectively (Rule et al. 2002). Feedlot bison tissues were comparable to those of range beef in their PUFA to SFA ratios (Rule et al. 2002), while feedlot beef tissues contained significantly less PUFA than the range beef tissues.

Comparing bison and beef, bison showed lower concentrations of myristic and palmitic acid, regardless of feeding regime (Rule et al. 2002). Linoleic acid content of bison was found to be higher than that of beef; this may be due to lower rates of biohydrogenation in bison. Overall CLA content was higher in range fed vs. feedlot animals (Rule et al. 2002). Species differences in CLA content varied by muscle sample but, generally, the content of range beef was greater than that of range bison, which was greater than that of feedlot bison, with feedlot beef having the lowest CLA content (Rule et al. 2002). Total saturated fat contents were comparable between range finished bison and beef, but the comparison is misleading as a greater proportion of the saturated fat in bison comes from stearic acid which has not been linked to influencing the LDL cholesterol levels in humans. Total fat content was found to be greatest in feedlot steers followed by feedlot bison, with range animals having the lowest levels (Rule et al. 2002).

Although there was some variation in fatty acid content among muscle groups in the study by Rule et al. (2002), feeding group and species had a greater influence. Differences in fatty acid composition have been noted between "red" and "white" muscle fiber types. Wood et al. (2003) stated that "red" muscle such as the gluteobiceps, contained higher proportions of phospholipids than "white" muscle, such as the *longissimus*. White muscle fibers tend to be larger than red muscle fibers. The red muscle fibers refer to cells containing smaller muscle fibers, which result in proportionally more cell membrane area, thus more phospholipids.

2.3.9. Critical Control Point for Fatty Acid Influence

Although species, genetics, age, and seasonal differences can all influence the fatty acid profile of ruminant tissues, it is the diet that has repeatedly been shown to have the greatest impact (French et al. 2000; Rule et al. 2002; Bolte et al. 2002; Griswold et al. 2003; Mir et al. 2004). The microbial activity of the rumen plays an important role in the biohydrogenation of dietary lipids. The diet of the animal is the most critical control point when trying to influence the fatty acid profile of the animal products. As human health concerns encourage a shift in ruminant product content, further emphasis will be placed improving the fatty acid profile.

Extrapolations based on previous studies using either beef or bison would suggest feeding management can have an effect on the fatty aid profile of ruminant tissues. Comparisons using either bison or beef indicate that forage based diets promote leaner tissue with a greater proportion of polyunsaturated fatty acids, in particular of the omega-3 group, compared to grain fed controls.

High concentrate finishing diets generally increases the deposition of intramuscular fat within beef muscle tissue as the animal nears physiological maturity. Resulting shifts in the fatty acid profile indicate an increase in saturated and monounsaturated fatty acid content, making the tissue profile more similar to that of subcutaneous tissue. Bison feedlot trials show a similar shift, but to a lesser extent than found with beef trials. Cattle have been genetically selected of for faster growth and more carcass fat than bison. Comparison of bison to beef on high grain rations exploits the species differences, while forage finishing tends to reduce species differences.

2.4. Summary and Objectives of Research

There are many questions regarding the nutritional management of bison and the role nutrition has in regard to bison meat products. Lipid content and profile of meat products are important from a human health perspective. Extrapolations of previous studies using either beef or bison suggest feeding management can have an effect on the fatty acid profile of ruminant tissues. Comparisons amongst bison indicate that forage based feeding systems promote leaner tissue with a greater proportion of polyunsaturated fatty acids. The effects of short term concentrate feeding have shown that a shift from a forage based diet to a high concentrate diet can affect the fatty acid profile of beef tissues. Higher concentrate finishing diets result in a greater deposition of marbling within beef, increasing both the saturated and monounsaturated fatty acid content of the beef tissues. Bison feedlot trials within the United States have shown a similar shift in the fatty acid profile of the tissues, but to a lesser extent. To date, no studies have been published investigating the feeding practices of bison within Canada.

The objectives of this study were:

1. To compare the fatty acid profiles of bison finished under four common commercial feeding programs found in western Canada.
2. To compare the fatty acid profiles of intensively fed bison bulls to those of intensively fed beef steers and sheep wethers.
3. To compare the fatty acid profiles of bison bulls to that of sheep wethers fed under forage finishing programs.

Based on the fatty acid profile of the tissues and how the profile relates to our current understanding to the effects these fatty acids have on human health, recommendations are made regarding the most desirable bison finishing program. Comparison of bison to other ruminants commercially produced in western Canada provides a relative ranking of bison tissue to that of other ruminants from a human health perspective.

3.0 Evaluation of the Effect of Dietary Forage and Concentrate Levels on the Fatty Acid Profile of Bison

3.1. Introduction

The bison industry is a growing niche market in the Saskatchewan livestock sector. To date there has been very little information gathered on the scope of the industry and its potential. Although there are estimates to the number of animals being finished in Saskatchewan, no one has investigated the types of finishing programs currently in operation. The primary focus of bison finishing production is the growing meat market. To establish a stable market for a product, the value of the product must be explored. The high content of saturated fatty acids and the negative connotations associated with them are detrimental to the promotion of ruminant meat products. Only a few published studies have explored the nutritional value of bison meat. Marchello and Driskell (2001) measured the differences in nutrient composition of grass- and grain-finished bison. Grass finished animals contained less fat, but more saturated fatty acids than grain finished bison. The ratio of polyunsaturated to saturated fatty acids was higher in grass than grain fed bison. Comparisons of other nutrients, such as protein (Table 2.1) and minerals (Table 2.2), found very little differences between grass or grain finished bison. Overall, bison meat was found to be a low-fat, low sodium, nutrient dense food. A study conducted by the University of Wyoming (Rule et al. 2001) compared the fatty acid composition of range to that of feedlot finished bison and cattle as well as the profile of elk. Comparisons were made between three different muscles of the ruminant species to that of chicken breast. Range finished beef, bison and elk all had similar omega-6 to omega-3 fatty acid ratios. The saturated fatty acid content of beef and bison under range or feedlot finishing conditions was similar. However, the PUFA content of the range fed animals was significantly higher than their feedlot finished counterparts. Conclusions drawn from the study indicate that the fatty acid profile of range fed bison is most similar to that of range fed beef or elk.

Finishing program comparisons for fatty acid profiles of ruminants usually focus on the extremes, either forage or feedlot finished. Indications from a survey of Saskatchewan producers illustrated the need to investigate the effects of a combination of forage and concentrates at different levels during the finishing period on the fatty acid profile of muscle tissue and main adipose storage sites. For the purpose of this study, the bison finishing period was defined as the time between weaning and slaughter. Identification and classification of the gray area between forage and feedlot finishing is necessary to understand the diversity of Saskatchewan finishing operations. The importance of diet and what impact it has on the bison tissues will further the understanding of how management can influence the meat product.

The objective of this study was to collect tissue samples from bison finished under a variety of finishing programs utilizing different levels of forage or concentrates during the finishing period. Analysis of subcutaneous and perirenal adipose tissue along with intramuscular tissue will demonstrate the effect of finishing strategy on the fatty acid profile of bison tissue.

3.2. Materials and Methods

Producers were selected based on their reported finishing practices during an initial phone and subsequent mail survey of all known bison producers in Saskatchewan in 2001. Finishing practices as defined for use in the survey portion of the study categorized the animals for subsequent tissue sample collection.

There were four management classifications for finishing bison used during this study, defined as follows:

1. Forage Fed (n=19) - bison remained on some type of forage, grass or legume throughout the finishing period. Bison were sampled from four producers and ranged in age from 16 to 28 months at the time of slaughter.
2. <90 Day Fed (n=9) - bison were fed on pasture, and then switched to a high grain diet for less than 90 days prior to slaughter. Bison were sampled from three producers and ranged in age from 19 to 28 months at the time of slaughter.

3. 50:50 Forage:Grain (n=20) - bison spent the entire finishing period on pasture, but had free choice access to concentrates during that period. Bison were sampled from five producers ranging in ages from 22 to 32 months at slaughter.
4. Feedlot Finishing (n=12) - bison were fed and housed under similar conditions as found in traditional North American beef feedlot operations. Feeding management of bison in the Feedlot Finishing treatment consisted of high-energy concentrate diets with free-choice conserved forage. Bison were sampled from four producers and ranged from 16 to 25 months of age at slaughter.

Pasture types included a mixture of native prairie, legume or grass varieties, usually in a rotational grazing combination. Primary ingredients of the high concentrate diets reported fed by bison producers included: barley, oat, and cereal grain screening pellets. The one exception was a feedlot producer who fed a total mixed ration containing cereal grain, pulse crop, and oil seed screenings along with cereal silage.

Sample size per finishing group varied as the number of producers willing to commit animals was subject to economic conditions and slaughter plant availability.

Samples from the selected study animals were collected over a period of two years. The area from which the bison selected for sampling came from covered the prairies from Winnipeg, MB, to Grand Prairie, AB. No two producers fed identical diets although they were selected from predefined categories. An effort was made to collect a minimum of three animals from each producer. The group of animals collected from each producer was usually slaughtered at one time. When same day slaughter was not a possibility, slaughter dates ranged up to a few months. Variation in season of slaughter and age of animals within groups were uncontrollable factors in this study and may influence the fatty acid profiles of the tissues. Bison were slaughtered in either provincially inspected abattoirs or killed on farm, the end point used for selection of slaughter animals was subject to producer discretion based on carcass size and estimated finish, similar to practices found for commercial endpoints of other domestic animal finishing programs.

3.2.1. Subcutaneous and Perirenal Tissue Collection

At the time of slaughter, a subcutaneous fat sample was removed from the carcass at the shoulder region. The perirenal fat sample was collected by peeling the fat from around one or both kidneys. Once collected, the samples were labeled, vacuum packed (Tilia Foodsaver Vac 550) in plastic bags (Tilia Foodsaver 18cm custom size bags), and placed on ice and transported to the University of Saskatchewan where they were placed in a -20°C freezer until analysis.

At the time of analysis, fat samples were cut into two-cm-thick sections while frozen. All exposed edges were trimmed roughly 0.5 cm to remove any surface that had been exposed to air for prolonged periods. The remaining pieces were cubed, placed in a glass jar and submersed in N_2 then freeze-dried using a Labconco Lyphlock 12 freeze dryer at -5°C for a minimum of seventy-two hours. Freeze dried samples were then ground in a household coffee grinder (Braun Aromatic model KSM 2), placed in snap cap plastic tubes, submersed in N_2 and stored at -20°C until extraction.

3.2.2. Intramuscular Tissue Collection

Hanging time of the carcasses varied from five to sixteen days. After the carcass had hung for the appropriate time requested by the producer, meat samples were collected at processing. Muscle samples were collected from the 12th rib of the ribeye (*longissimus dorsi*) area. Once collected, the samples were labeled, vacuum packed (Tilia Foodsaver Vac 550) in plastic bags (Tilia Foodsaver 18cm custom size bags), and placed on ice and transported to the University of Saskatchewan, where they were stored at -20°C until analysis. At the time of analysis, ribeye samples were cut into two-cm-thick sections while frozen. All exposed edges were trimmed roughly 1 cm to remove any surface that was exposed to air for prolonged periods. The remaining sample was cubed, placed in a glass jar and submersed in N_2 then freeze dried using a Labconco Lyphlock 12 freeze dryer at –5°C for a minimum of seventy-two hours. Freeze dried samples were then ground in a household coffee grinder (Braun Aromatic model KSM 2), placed in snap cap plastic tubes, submersed in N_2 and stored at -20°C until extraction.

3.2.3. Lipid Extraction

Lipid extraction was done by following the methods of Bligh & Dyer (1959). Powdered muscle tissue (1.0 g) or powdered fat tissue (100 mg) was weighted, and placed into a 250 mL Erlenmeyer flask. Double distilled water (1 mL) was added to the powdered muscle tissue samples to increase moisture content to 80%. An internal triglyceride marker, (trihenicosanoin, Nu-chek) was added at a volume of 500 μl per sample at a concentration of 41.6 mg 10 mL^{-1} chloroform. The internal marker for the subcutaneous and perirenal samples was methylated tetracosanoic acid (Nu-chek) at 500 μL per sample with a concentration of 40 mg 10 mL^{-1} chloroform. Using a serological pipet (VWR), 25 mL chloroform (Omnisolv, EDM) was added. Then 50 mL of methanol was added to the sample. The sample was homogenized for two minutes using a Brinkmann 10/35 Polytron. Another 25 mL chloroform was added and homogenized for thirty seconds. Twenty-five milliliters of double distilled water was added and homogenized for thirty seconds. Finally, 35.5 mL chloroform was added and homogenized for one minute. Between samples, the Polytron shaft was rinsed with a small amount of chloroform to prevent cross contamination of the samples. The homogenate was filtered through a porcelain Hirsch funnel (Coors U.S.A.) lined with Whatman 3.2-cm no.1 filter paper, with slight suction, into a 250 mL filtering flask. The Erlenmeyer flask was rinsed twice with 5 mL chloroform each time and poured on the filter paper to flush through any fat residue. The filtering flask was allowed to sit for a few seconds to allow as much solvent to be sucked through the filter paper as possible. The filtered solvent was then placed into a 250-mL separatory funnel (Pyrex), the filter flask was rinsed once with 5 mL chloroform. The solvent was allowed to sit for a minimum of twelve hours to allow the layers to separate fully. Once the layers were fully separated, the bottom layer was gravity filtered through a glass funnel lined with Whatman 110-mm no.1 filter paper filled with 1 gm of anhydrous sodium sulphate, into a 100-mL glass cylinder. A small amount of solvent was left in the separatory funnel to avoid contamination with the water/methanol mixture in the top layer. Once filtered, the solvent was placed in a hot water bath at 40°C, under a steady stream of N_2. The chloroform was allowed to evaporate until there was roughly 10 mL left. The remaining solvent was then transferred via glass pipet to a pre-weighed, pre-washed 15-mL screw top culture tube. The remaining solvent was then evaporated under a steady flow of N_2 until a stable weight was attained. The final weight was recorded and used as a final extracted fat weight. Extracted lipid was then flushed once more with N_2 sealed with Teflon lined screw caps, and stored in a -20°C freezer until methylation.

3.2.4. Methylation of Extracted Lipid

Methylation followed a modification of the base/acid catalyzed reaction of Lock and Garnsworthy (2002). The sealed culture tubes were removed from the freezer and placed in a water bath at room temperature. The water bath was then heated to 40°C. To each culture tube, 50 µL of hexane was added and then vortexed to re-suspend the lipid extract. Using a serological pipet and portable pipet-aid (Drummond), 2 mL of 0.5 *M* sodium methoxide (Sigma-Aldrich) was added in 1mL aliquots to each culture tube. Tubes were flushed with N_2, resealed and vortexed thoroughly for thirty seconds. The culture tube was then placed in a 50°C water bath for fifteen minutes. The culture tubes were then removed from the water bath and briefly vortexed. Culture tubes were then allowed to cool to room temperature before proceeding. One milliliter of boron triflouride (14% in methanol) (Sigma-Aldrich) was then added to each culture tube, flushed with N_2, resealed and vortexed for thirty seconds. The tubes were then placed back into the 50°C water bath for fifteen minutes. The tubes were then removed from the water bath, vortexed briefly and allowed to cool to room temperature. To each culture tube, 5 mL of double distilled water was added, flushed with N_2, sealed and vortexed for fifteen seconds. To each culture tube, 1900 µL of hexane was added, along with 100 µL of methylated nonadecanoate (Nu-Chek) at a concentration of 10 mg mL^{-1} hexane. Tubes were flushed, re-capped and vortexed thoroughly for fifteen seconds to allow all lipids to transfer to the hexane layer. Culture tubes were then centrifuged (Beckman J6-MC) at 2560 *g* for ten minutes to facilitate the separation of the layers. Roughly three-quarters of the hexane/lipid layer was transferred to another pre-washed screw top culture tube using a glass pipet. The tube was again flushed with N_2, capped and centrifuged at 4550 *g* for fifteen minutes in order to remove any suspended particle matter. Roughly 500 µL of the hexane/lipid solution was transferred to an amber screw top gas chromatography vial, flushed with N_2, and stored at -20°C until run on the gas chromatograph (GC).

3.2.5. Gas Chromatograph Methodology

Fatty acid separation was obtained using a Gas Liquid Chromatograph (GLC), Agilent model 6890 with autosampler (Agilent 7683). The GLC was fitted with a 100-m capillary column (SP 2560, Supelco) set at a split ratio of 100:1. The carrier gas used was He at a column flow rate of 15 cm s^{-1} (0.7 mL min^{-1}). Injector temperature was set at 220°C and the detector at 250°C. Column temperature was held at 175°C for 73.00 minutes, then ramped to 225°C at 4°C min^{-1}, then held for 35.00 minutes.

Purified standards of thirty-six methylated fatty acids (Appendix A) were obtained from Nu-Chek Prep, Inc. Elysian, MN, USA. Liquid standards contained a minimum of 100 mg per tube. Standards were extracted from their vials, rinsed with hexane using three 500 µL flushes and places in a glass vial. The vials were then dried under N_2, weighed, and then re-suspended in 2 mL hexane. Concentrations of standard per mL of hexane were recorded. Four standards of different chain length or clearly separable degrees of unsaturation were placed into six vials at 240 µL each and two vials with 120 µL of each standard. To each vial, 40 µL of internal standard at 5 mg mL^{-1} concentration was also added to allow for correction if there was injection error. This was to allow for a "shotgun" approach to determining the slope of each standard. Plotting six points at a high concentration, along with two points at a half dilution, then taking the average of the points and forcing the line through zero, achieved the slope of the standards. Retention times of the reference standards were used as the basis for identifying the individual fatty acid methyl ester (FAME) peaks in the experimental samples.

Tissue samples were run in groups of twelve with a hexane flush followed by a reference standard (GLC 461, Nu-Chek) at the beginning of each set to monitor system shifts in elution time.

3.2.6. Statistical Analysis

Data was analyzed using the PROC MIXED procedures of SAS (SAS Inst., Inc., Cary, NC.). The statistical model for fatty acid composition for bison included the effect of treatment, tissue type and the interaction for treatment x tissue type. When interaction effects occurred, slices were used to separate simple means. Both main and simple effects were evaluated with least square difference separation. Mineral analysis of liver tissue was analyzed as a one-way ANOVA for treatment. An α level of P=0.05 was specified for significance.

3.3. Results

Lipid yield from freeze dried ribeye tissue extraction for intramuscular lipid was as follows: Grass Fed (0.0529 g g^{-1} tissue DM), <90 Day Fed (0.0687 g g^{-1} tissue DM), 50:50 Forage:Grain (0.0544 g g^{-1} tissue DM), Feedlot Finishing (0.0709 g g^{-1} tissue DM).

3.3.1. Fatty acids from C14's to C17's Chain Length

14:0 Myristic

There was an interaction (P<0.05) between treatment and tissue type for myristic acid (Table 3.2.). Within subcutaneous tissue, simple effects (P>0.05) show the Forage Fed, <90 Day Fed and Feedlot Finishing treatments were similar (P>0.05), all treatments having a greater (P<0.05) myristic acid content than the 50:50 Forage:Grain treatment (Fig. 3.1.). Simple effects (P<0.05) for treatment within perirenal tissue show the Forage Fed treatment contained more (P<0.05) myristic acid than the <90 Day Fed or 50:50 Forage:Grain treatments, which were similar (P>0.05). The Feedlot Finishing group was intermediate between Forage Fed and the other treatments for myristic acid content in the perirenal tissue. Simple effects (P<0.05) for treatments within intramuscular tissue indicated that the Feedlot Finishing treatment contained a greater (P<0.05) content of myristic acid than the other three treatments (Fig. 3.1.). Separation of simple effects (P<0.05) for tissue differences within treatments show subcutaneous and perirenal tissue being similar (P>0.05), both having a greater (P<0.05) content of myristic acid than found in intramuscular tissue across all four treatments (Fig. 3.2.).

16:0 Palmitic

Effects (P<0.05) for tissues indicate that subcutaneous and perirenal tissues have similar (P>0.05) palmitic acid content, both contained greater (P<0.05) amounts than found in intramuscular tissue (Table 3.1.). Effects (P<0.05) for treatments show palmitic acid content being similar (P>0.05) for the Forage Fed, <90 Day Fed and Feedlot Finishing treatments. All three treatments had greater (P<0.05) palmitic acid content than the 50:50 Forage:Grain treatment (Fig. 3.3.).

Table 3.1. Main effects for the fatty acid profile of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison fed under four different finishing strategies

		Treatment[z]					Tissue[z]				
		Forage Fed	<90 Day Fed	50:50 Forage:Grain	Feedlot Finishing	P SEM	Subcutaneous	Perirenal	Intramuscular	P SEM	Effect
Fatty Acid		mg g^{-1} total fatty acid methyl esters									
14:0	Myristic	27.66	26.00	23.09	27.95	0.78	31.81	31.47	15.25	0.77	*c*
14:1 *c*-9	Myristoleic	2.11	1.95	1.82	2.08	0.13	1.50 e	0.59 f	3.88 d	0.13	*b*
15:0	Pentadecanoic	23.06	13.51	19.94	12.37	1.60	7.59	6.88	37.18	1.58	*c*
16:0	Palmitic	220.34 d	230.18 d	201.87 e	222.32 d	4.32	236.65 d	234.22 d	185.16 e	4.26	*ab*
16:1 *c*-9	Palmitoleic	26.01	24.48	24.93	25.89	0.92	32.16 d	22.88 e	20.94 e	0.91	*b*
17:0	Margaric	26.77	22.45	28.36	19.58	1.25	19.95	22.36	30.58	1.23	*c*
17:1 *c*-9	Heptadecenoic	3.60	3.58	3.38	3.06	0.17	5.38 d	3.01 e	1.82 f	0.17	*b*
18:0	Stearic	220.74	249.65	257.49	227.86	5.80	239.47	343.77	133.56	5.72	*c*
18:1 *t*-9	Elaidic	4.60	2.36	2.41	1.66	0.42	2.15	3.05	3.09	0.42	*c*
18:1 *t*-11	*Trans* vaccenic	41.54	18.19	20.38	21.65	1.66	30.44	32.42	13.46	1.64	*c*
18:1 *c*-9	Oleic	287.62	310.41	311.26	355.08	7.17	343.81	251.82	352.66	7.08	*c*
18:1 *c*-11	Vaccenic	11.51	11.37	10.51	9.16	0.66	6.42 e	5.08 e	20.42 d	0.65	*b*
18:2 *c*-9,12	Linoleic	48.72	48.61	51.26	40.25	3.61	21.71	20.57	99.34	3.56	*c*
20:0	Arachidic	2.69	3.27	4.76	2.92	0.39	3.40	5.29	1.54	0.39	*c*
18:3 *c*-6,9,12	γ-linolenic	0.29 d	0.19 e	0.35 d	0.20 e	0.03	0.06 e	0.07 e	0.64 d	0.03	*ab*
20:1 *c*-11	Eicosenoic	0.67	0.53	0.24	0.27	0.11	0.40	0.22	0.67	0.11	*c*
18:3 *c*-9,12,15	α-Linolenic	18.62	13.51	8.83	9.92	0.93	9.93	9.90	18.34	0.92	*c*
18:2 *c*-9,t-11	CLA	5.79	5.13	2.88	3.49	0.23	5.54	3.64	3.79	0.22	*c*
18:2 *t*-10,*c*-12	CLA	0.03	0.01	0.06	0.02	0.02	0.02	0.02	0.04	0.02	
20:2 *c*-11,14	Eicosadienoic	0.47	0.41	0.52	0.38	0.05	0.17	0.13	1.04	0.05	*c*
22:0	Behenic	0.27	0.20	0.24	0.15	0.03	0.00	0.00	0.65	0.03	*c*
20:3 *c*-8,11,14	Homo-γ-linolenic	1.83 e	1.25 ef	2.42 d	1.06 f	0.23	0.83 e	1.29 e	2.79 d	0.23	*ab*
20:3 *c*-11,14,17	Eicosatrienoic	0.18	0.09	0.21	0.16	0.03	0.07 e	0.08 e	0.34 d	0.03	*b*
22:1 *c*-13	Erucic	0.40	0.36	0.23	0.28	0.04	0.24	0.18	0.54	0.04	*c*
20:4 *c*-5,8,11,14	Arachidonic	12.73	7.52	12.56	7.56	1.30	1.05	1.18	28.04	1.28	*c*
22:2 *c*-13,16	Docosadienoic	0.51 de	0.25 ef	0.59 d	0.17 f	0.10	0.22 e	0.24 e	0.67 d	0.10	*ab*
20:5 *c*-5,8,11,14,17	Eicosapentaenoic	2.62	1.05	1.76	0.71	0.23	0.14	0.13	4.34	0.23	*c*
22:4 *c*-7,10,13,16	Docosatetraenoic	0.72	0.49	2.17	0.56	0.68	0.32 e	0.12 e	2.51 d	0.67	*b*
22:5 *c*-7,10,13,16,19	Docasapentaenoic	6.14	2.48	3.75	2.03	0.48	0.88	0.57	9.36	0.47	*c*
22:6 *c*-4,7,10,13,16,19	Docosahexaenoic	1.71	0.83	0.87	0.57	0.15	0.07	0.02	2.90	0.15	*c*

a-b , means within main effect differ (P <0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (P <0.05), shown on Table 3.2.

d-f, means within a row are different (P <0.05) for each main effect.

[z] sample numbers for Forage Fed subcutaneous, perirenal, and intramuscular tissue, n=12; <90 Day subcutaneous, perirenal, and intramuscular tissue, n=9; 50:50 Forage:Grain subcutaneous, perirenal, and intramuscular tissue, n=20; Feedlot Finishing subcutaneous, perirenal, and intramuscular tissue, n=12.

Table 3.2. Interaction effects (*P* <0.05) for the fatty acid profile of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison fed under four different finishing strategies

		Forage Fed			<90 Day Fed			50:50 Forage:Grain			Feedlot Finishing			
		Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
Fatty Acid		mg g^{-1} total fatty acid methyl esters												
14:0	Myristic	34.37	34.49	14.12	32.94	29.51	15.56	26.92	29.90	12.45	33.01	31.99	18.86	1.42
15:0	Pentadecanoic	11.98	8.94	48.26	6.58	5.73	28.22	5.64	7.20	46.97	6.16	5.65	25.28	2.93
17:0	Margaric	22.93	26.00	31.40	20.06	21.72	25.58	19.12	22.47	43.49	17.68	19.24	21.84	2.28
18:0	Stearic	212.05	323.61	126.56	233.23	379.11	136.60	270.95	370.70	130.81	241.64	301.66	140.28	10.60
18:1 *t*-9	Elaidic	5.41	4.17	4.23	1.06	3.06	2.97	1.30	3.68	2.27	0.85	1.27	2.87	0.77
18:1 *t*-11	*T*-vaccenic	50.84	57.38	16.39	19.44	19.29	15.84	23.66	27.19	10.29	27.82	25.82	11.31	3.04
18:1 *c*-9	Oleic	328.88	229.20	304.79	333.46	220.02	377.74	356.93	247.96	328.90	355.96	310.07	399.22	13.11
18:2 *c*-9,12	Linoleic	17.18	17.19	111.79	24.85	25.65	95.32	22.17	16.40	115.20	22.64	23.03	75.07	6.59
20:0	Arachidic	2.51	4.41	1.17	2.29	4.97	2.55	5.50	7.43	1.35	3.31	4.36	1.08	0.72
20:1 *c*-11	Eicosenoic	1.06	0.42	0.53	0.38	0.29	0.91	0.04	0.07	0.63	0.11	0.10	0.61	0.20
18:3 *c*-9,12,15	α-Linolenic	12.06	13.07	30.75	12.31	11.35	16.88	6.21	6.07	14.21	9.14	9.10	11.52	1.70
18:2 *c*-9,*t*-11	CLA	7.85	4.45	5.06	6.55	4.15	4.69	3.88	2.49	2.29	3.86	3.49	3.12	0.42
20:2 *c*-11,14	Eicosadienoic	0.24	0.12	1.04	0.02	0.05	1.16	0.20	0.12	1.25	0.23	0.21	0.71	0.10
22:0	Behenic	0.80	0.72	0.60	0.46	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06
22:1 *c*-13	Erucic	0.20	0.21	0.78	0.22	0.17	0.68	0.23	0.12	0.34	0.30	0.20	0.35	0.08
20:4 *c*-5,8,11,14	Arachidonic	0.79	0.84	36.55	1.15	1.72	19.69	1.26	0.82	35.60	1.01	1.32	20.34	2.38
20:5 *c*-5,8,11,14,17	Eicosapentaenoic	0.19	0.16	7.52	0.07	0.11	2.98	0.25	0.21	4.81	0.04	0.03	2.05	0.43
22:5 *c*-7,10,13,16,19	Docasapentaenoic	1.35	0.89	16.19	0.29	0.34	6.82	1.41	0.66	9.19	0.46	0.38	5.25	0.88
22:6 *c*-4,7,10,13,16,19	Docosahexaenoic	0.13	0.03	4.96	0.02	0.00	2.47	0.07	0.02	2.51	0.05	0.03	1.64	0.28

[z] sample numbers for Forage Fed subcutaneous, perirenal, and intramuscular tissue, n=12; <90 Day subcutaneous, perirenal, and intramuscular tissue, n=9; 50:50 Forage:Grain subcutaneous, perirenal, and intramuscular tissue, n=20; Feedlot Finishing subcutaneous, perirenal, and intramuscular tissue, n=12.

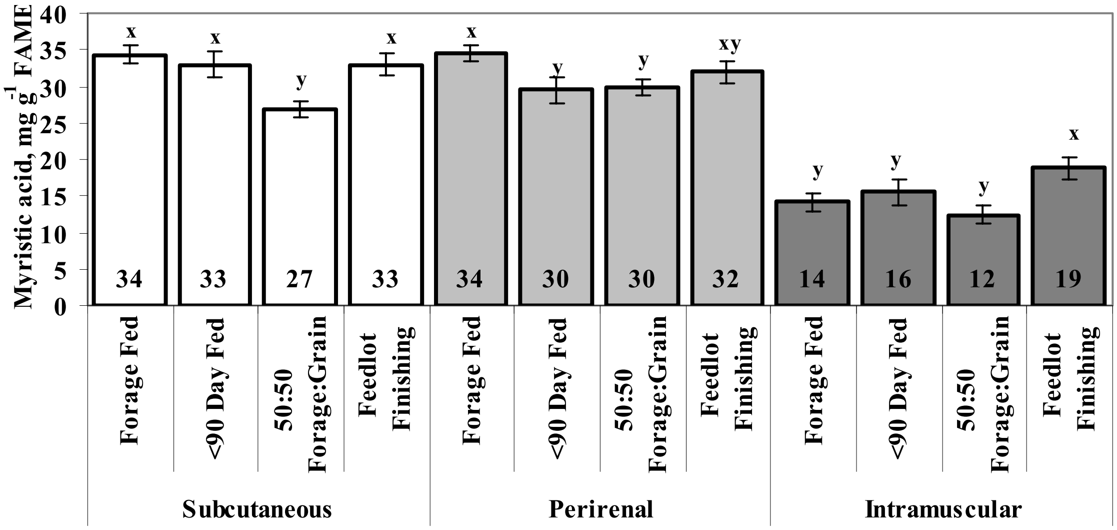

Figure 3.1. Dietary treatment x tissue type interaction for myristic acid (C14:0) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=1.19, <90 Day Fed=1.74, 50:50 Forage:Grain=1.16, Feedlot Finishing=1.50.

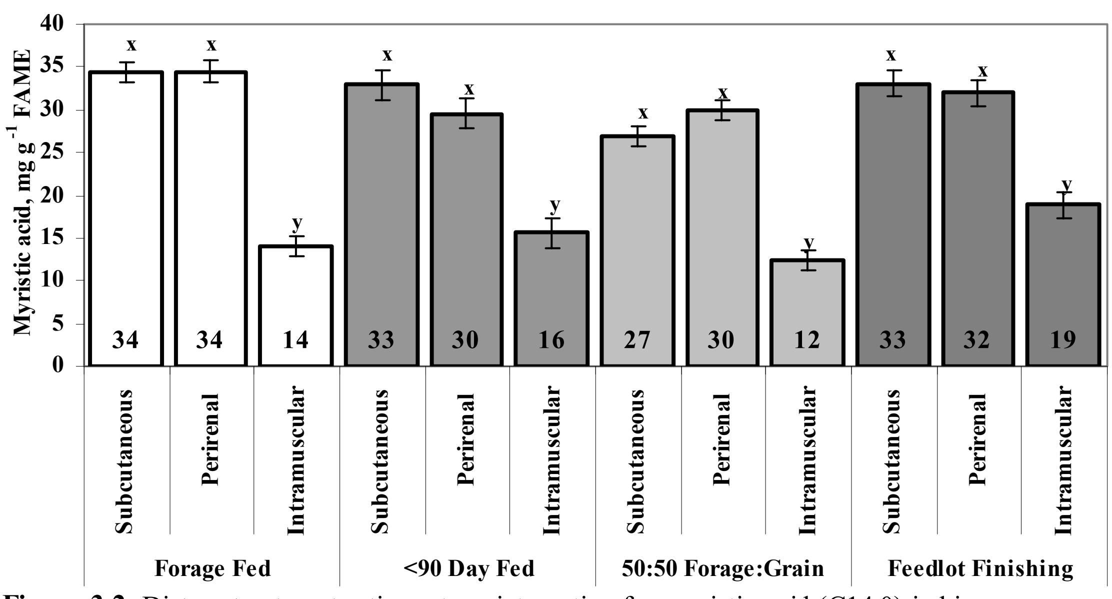

Figure 3.2. Dietary treatment x tissue type interaction for myristic acid (C14:0) in bison, means separation for tissue type within dietary treatment. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=1.19, <90 Day Fed=1.74, 50:50 Forage:Grain=1.16, Feedlot Finishing=1.50.

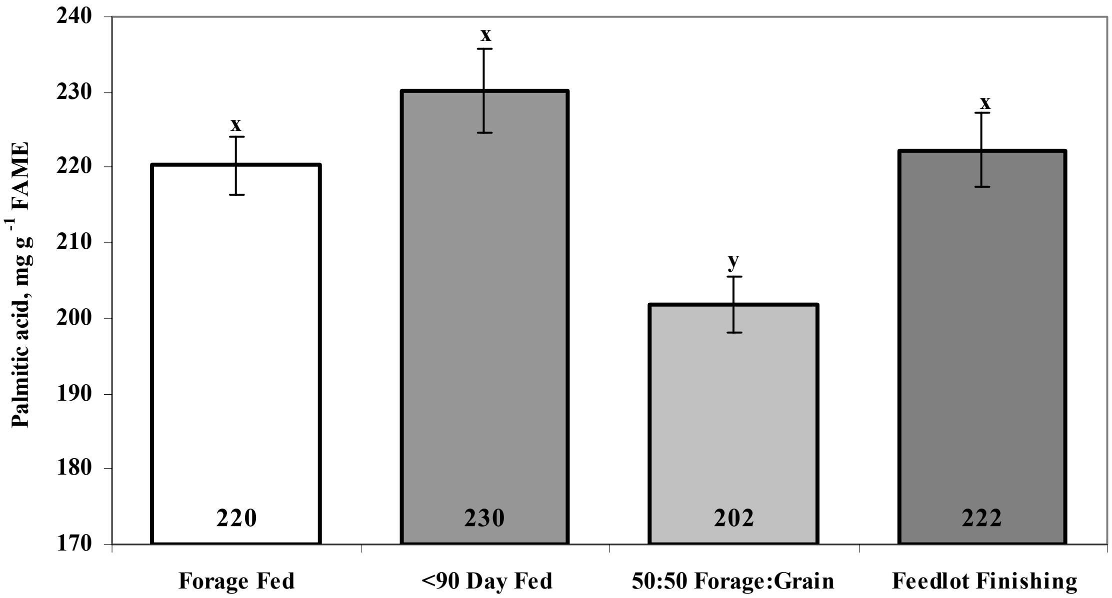

Figure 3.3. Effect of dietary treatment for palmitic acid (C16:0) in bison. Means between treatments followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=3.84,

Minor C14 to C17 Fatty Acids

Minor fatty acids identified with carbon chain length of 14 to 17 include myristoleic, pentadecanoic, palmitoleic, margaric and heptadecenoic acid. Effects (P<0.05) of tissue type show a greater (P<0.05) content of myristoleic acid in the intramuscular tissue compared to the subcutaneous or perirenal tissue (Table 3.1.). Effects (P<0.05) of tissue type for palmitoleic indicate a larger (P<0.05) portion to be found in subcutaneous tissue than either perirenal or intramuscular tissue (Table 3.1.).

Of the odd chain length fatty acids, pentadecanoic and margaric acid as well as its monounsaturated derivative, heptadecenoic acid, accumulated to a greater degree in the intramuscular tissue than in the other tissues (Table 3.1.). Evaluation of simple effects (P<0.05) for pentadecanoic acid show within intramuscular tissue, higher (P<0.05) levels were identified in the Forage Fed and 50:50 Forage:Grain treatment compared to the <90 Day Fed or Feedlot Finishing treatment, which were similar (P>0.05) (Table 3.2.). Separation of simple effects for treatments within tissues for margaric acid indicates the 50:50 Forage:Grain treatment to have the greatest (P<0.05) content followed by the Forage Fed, with the Feedlot Finishing treatment having the least (P<0.05) margaric acid content (Table 3.2.). The margaric acid content of the <90 Day Fed treatment was similar (P>0.05) to both the Forage Fed and Feedlot Finishing treatments (Table 3.2.). Effects (P<0.05) of tissue for heptadecenoic acid show the greatest (P<0.05) amount in subcutaneous tissue, followed by perirenal tissue, with intramuscular tissue having the least (P<0.05) heptadecenoic acid (Table 3.1.). There were no treatment differences for heptadecenoic acid.

3.3.2. Saturated and Monounsaturated Fatty Acids of C18 Chain Length

18:0 Stearic

There was an interaction effect (P<0.05) between treatments and tissues for stearic acid (Table 3.2.). Separation of simple effects (P<0.05) of treatments within subcutaneous tissue show the 50:50 Forage:Grain treatment to have the greatest (P<0.05) amount of stearic acid, followed by the Feedlot Finishing treatment, with the Forage Fed treatment having the least (P<0.05), (Fig. 3.4.). The <90 Day Fed treatment was intermediate (P>0.05) to the Feedlot Finishing and Forage Fed treatments. Simple

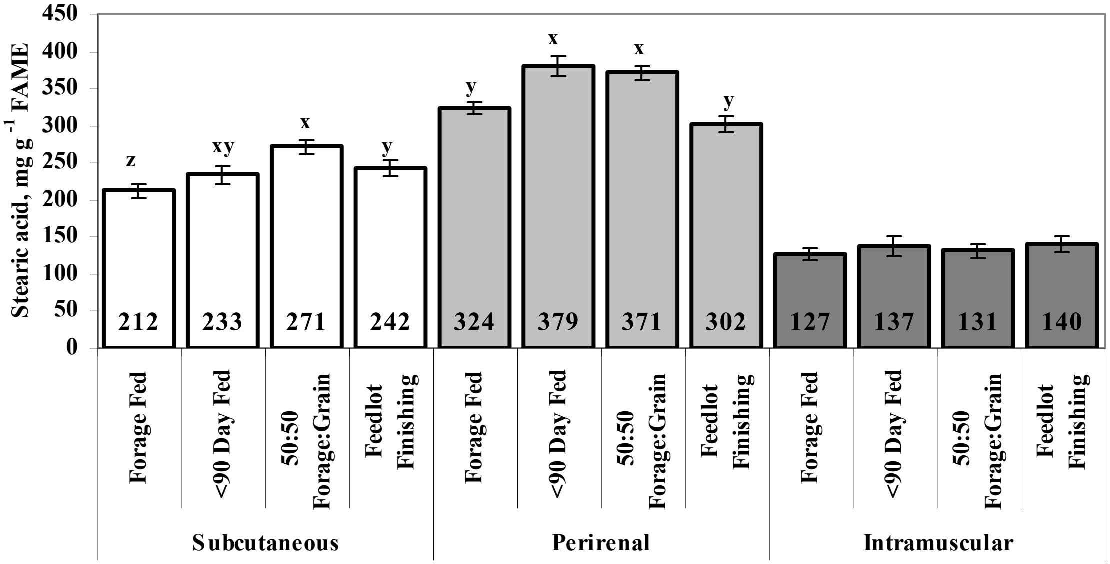

Figure 3.4. Dietary treatment x tissue type interaction for stearic acid (C18:0) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=8.93, <90 Day Fed=12.97, 50:50 Forage:Grain=8.70, Feedlot Finishing=11.23.

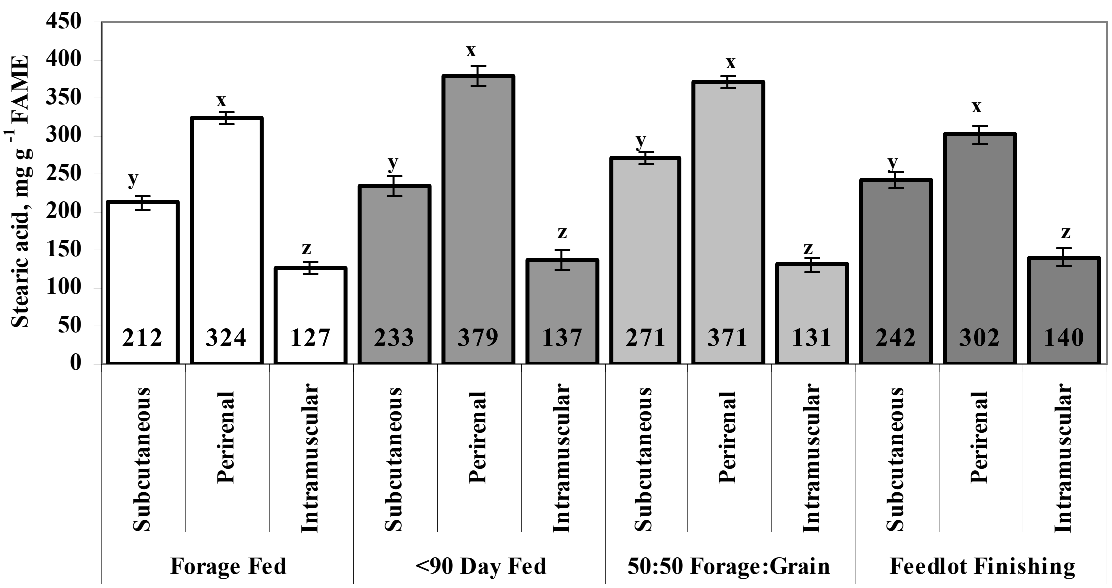

Figure 3.5. Dietary treatment x tissue type interaction for stearic acid (C18:0) in bison, means separation for tissue type within dietary treatment. Means within treatment followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=8.93, <90 Day Fed=12.97, 50:50 Forage:Grain=8.70, Feedlot Finishing=11.23.

effects ($P<0.05$) of treatments within perirenal tissue, indicate the stearic acid content was similar ($P>0.05$) between the <90 Day Fed and 50:50 Forage:Grain treatments, which was greater ($P<0.05$) than the Forage Fed and Feedlot Finishing treatments (Fig 3.4.). Simple effect ($P<0.05$) separation of tissues within treatments indicates a greater ($P<0.05$) content of stearic acid to be found in perirenal tissue, followed by subcutaneous tissue, with the least ($P<0.05$) amount in the intramuscular tissue (Table 3.2.), (Fig. 3.5.).

18:1 *t*-11 *Trans*vaccenic

An interaction effect ($P<0.05$) between treatments and tissues was observed for the content of *trans*vaccenic acid (Table 3.2.). Simple effects ($P<0.05$) show that within both subcutaneous and perirenal tissues, there was a greater ($P<0.05$) content of *trans*vaccenic acid in the Forage Fed treatment than in the other three treatments, which were similar ($P>0.05$) to each other (Fig. 3.6.). Separation of simple effects ($P<0.05$) for tissues within treatments indicate a greater ($P<0.05$) amount of *trans*vaccenic acid can be found in the subcutaneous and perirenal tissues compared to the intramuscular tissue for all treatments (Fig. 3.7.), except the <90 Day Fed where there were no tissue differences ($P>0.05$).

18:1 *c*-9 Oleic

There was an interaction ($P<0.05$) between treatments and tissue type for oleic acid (Table 3.2.). Within perirenal tissue, simple effects ($P<0.05$) indicate the Feedlot Finishing treatment contained more ($P<0.05$) oleic acid than the other three treatments, which were indistinguishable ($P>0.05$) from each other. Separation of simple effects ($P<0.05$) for oleic acid for treatment within intramuscular tissue, indicate the <90 Day Fed and Feedlot Finishing treatments were similar ($P>0.05$), both containing greater ($P<0.05$) amounts than found in either the Forage Fed or 50:50 Forage:Grain treatments, which were also similar ($P>0.05$) (Fig. 3.8.). Simple effects ($P<0.05$) of tissue within treatment show the oleic acid content of subcutaneous and intramuscular tissue to be similar ($P>0.05$), both being greater ($P<0.05$) than the perirenal tissue

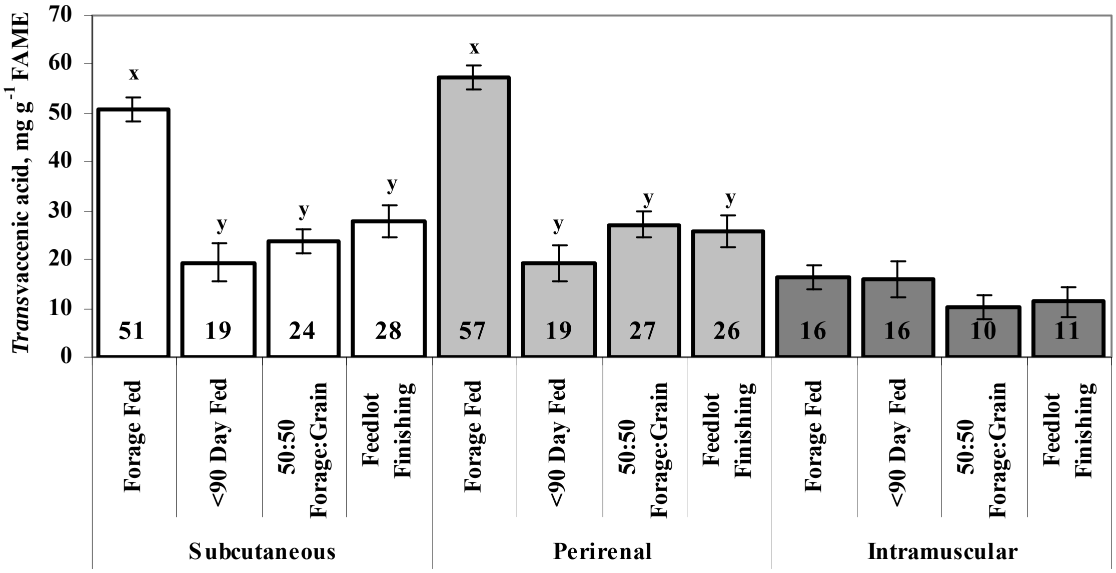

Figure 3.6. Dietary treatment x tissue type interaction for *trans* vaccenic acid (C18:1, *t*-11) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=2.56, <90 Day Fed=3.72, 50:50 Forage:Grain=2.49, Feedlot Finishing=3.22.

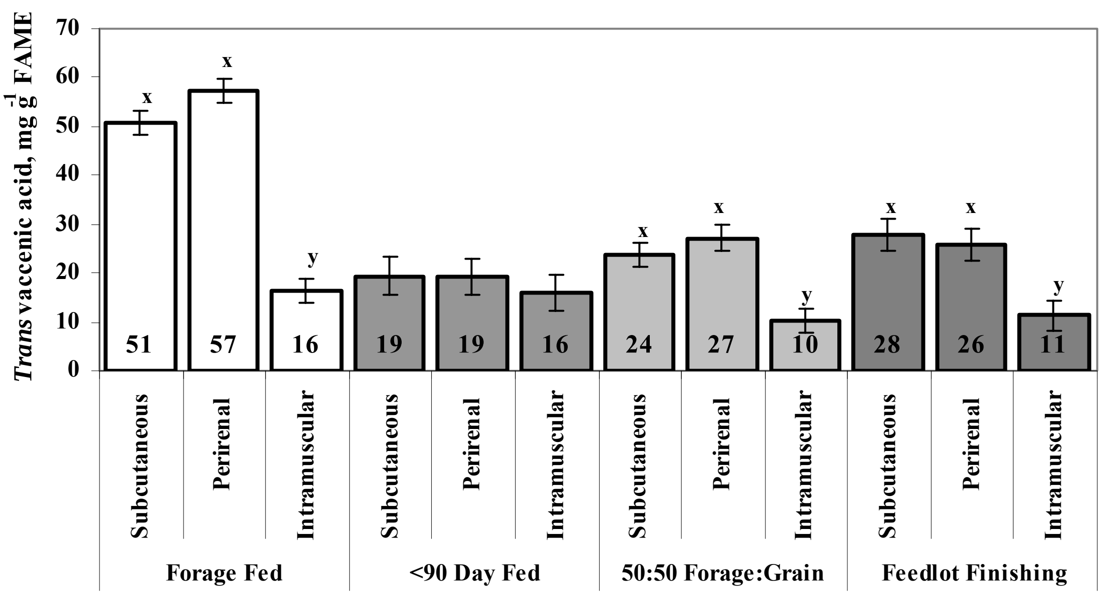

Figure 3.7. Dietary treatment x tissue type interaction for *trans* vaccenic acid (C18:1 *t*-11) in bison, means separation for tissue type within dietary treatment. Means within treatment followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=2.56, <90 Day Fed=3.72, 50:50 Forage:Grain=2.49, Feedlot Finishing=3.22.

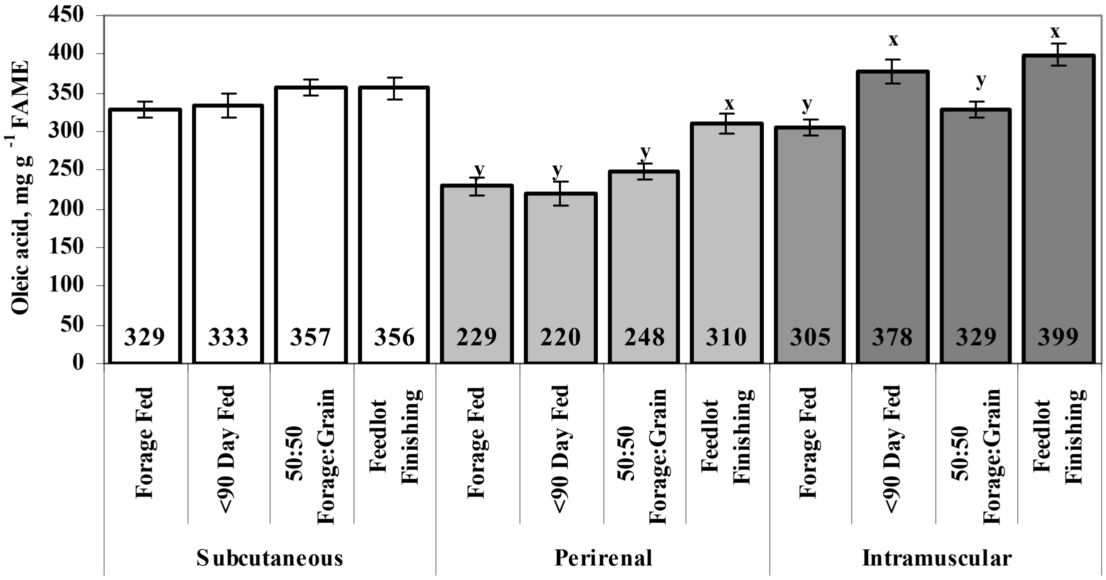

Figure 3.8. Dietary treatment x tissue type interaction for oleic acid (C18:1 *c*-9) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=11.04, <90 Day Fed=16.03, 50:50 Forage:Grain=11.76, Feedlot Finishing=13.89

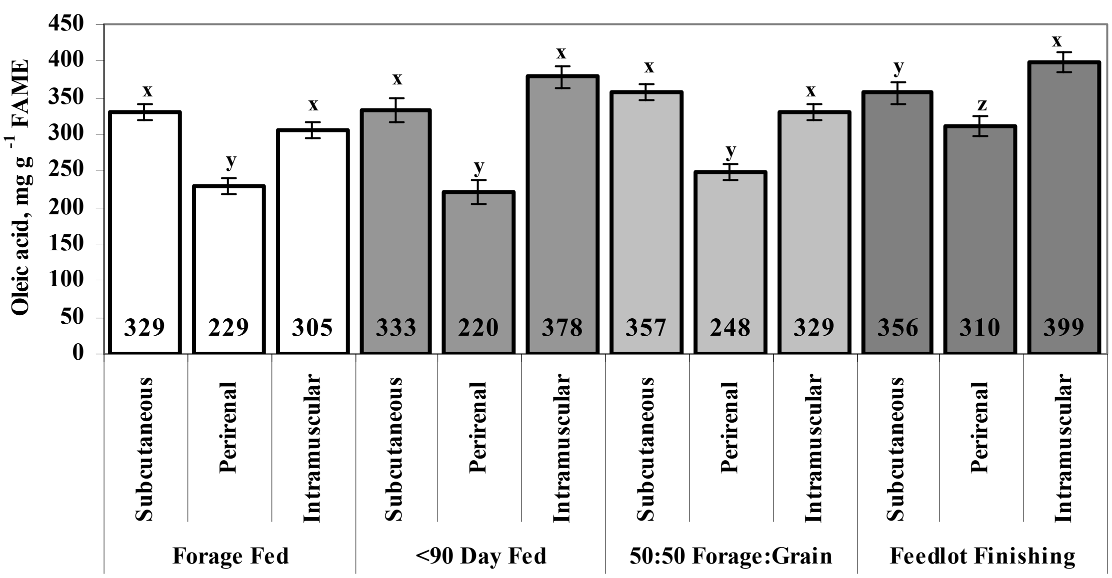

Figure 3.9. Dietary treatment x tissue type interaction for oleic acid (C18:1 *c*-9) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=11.04, <90 Day Fed=16.03, 50:50 Forage:Grain=11.76, Feedlot Finishing=13.89.

content for all treatments except the Feedlot Finishing treatment, where intramuscular tissue had slightly more ($P<0.05$) oleic acid than did subcutaneous tissue (Fig. 3.9.).

Minor C18 Fatty Acids

Minor C18 monounsaturated fatty acids identified include elaidic and vaccenic acid. An interaction ($P<0.05$) of treatment by tissue types was identified for elaidic acid (Table 3.2.). Within subcutaneous tissue, simple effects ($P<0.05$) indicate more ($P<0.05$) elaidic acid was found in the Forage Fed treatment than the other three treatments, which were comparable ($P>0.05$). Evaluation of simple effects ($P<0.05$) for perirenal tissue showed higher ($P<0.05$) levels of elaidic acid in the Forage Fed and 50:50 Forage:Grain treatments than found in the Feedlot Finishing treatment, with the <90 Day Fed treatment being similar ($P>0.05$) to all treatments (Table 3.2.). Separation of simple effects ($P<0.05$) for tissues within treatment showed within the 50:50 Forage:Grain treatment, the elaidic acid content was higher ($P<0.05$) in the perirenal tissue than the subcutaneous tissue, with intramuscular tissue being intermediate ($P>0.05$). Effects ($P<0.05$) of tissue type indicated more ($P<0.05$) vaccenic acid in intramuscular tissue than subcutaneous or perirenal tissue (Table 3.1.).

3.3.3. C18 Diunsaturated, Conjugated Linoleic Acid and Polyunsaturated

18:2 *c*-9, 12 Linoleic

There was an interaction ($P<0.05$) between treatments and tissue types for linoleic acid (Table 3.2.). Simple effects ($P<0.05$) indicated that within intramuscular tissue, the 50:50 Forage:Grain treatment contained the most ($P<0.05$) linoleic acid followed by the <90 Day Fed treatment, with the Feedlot Finishing treatment having the least ($P<0.05$), (Fig. 3.10.). The Forage Fed treatment was intermediate ($P>0.05$) between the 50:50 Forage:Grain and <90 Day Fed treatments. Within treatments, separation of simple effects ($P<0.05$) indicates intramuscular tissue to have a greater ($P<0.05$) amount of linoleic acid content than either the subcutaneous or perirenal tissues.

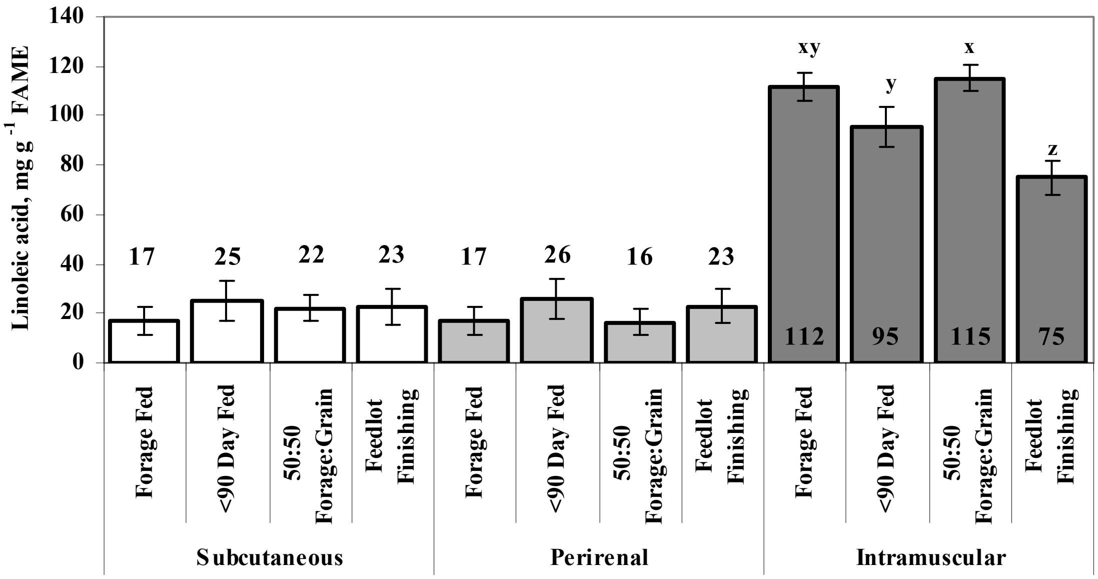

Figure 3.10. Dietary treatment x tissue type interaction for linoleic acid (C18:2 *c*-9, 12) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=5.55, <90 Day Fed=8.06, 50:50 Forage:Grain=5.41, Feedlot Finishing=6.98.

18:3 α-Linolenic

There was a treatment by tissue type interaction identified for α-linolenic acid (Table 3.2.). In both subcutaneous and perirenal tissues, simple effects ($P<0.05$) show the α-linolenic acid content for the Forage Fed and <90 Day Fed treatments was equivalent ($P>0.05$), both containing more ($P<0.05$) α-linolenic acid than the 50:50 Forage:Grain treatment (Fig. 3.11.). The content of α-linolenic acid found in both the subcutaneous and perirenal tissue of the Feedlot Finishing treatment was similar ($P>0.05$) to the other three treatments. In the intramuscular tissue, treatment effects indicated that the α-linolenic content was greater ($P<0.05$) in the Forage Fed treatment than in the other three treatments, which were similar ($P>0.05$). Tissue differences within treatments were only identifiable in the Forage Fed and 50:50 Forage:Grain treatments, where the α-linolenic acid content was greater ($P<0.05$) in intramuscular tissue than in either subcutaneous or perirenal tissue.

Conjugated Linoleic Acid Isomers

Interaction effects for treatments and tissue types were observed for the dominant Conjugated Linoleic Acid (CLA) isomer, 18:2 *c*-9, *t*-11 (Table 3.2.). Within subcutaneous tissue, the Forage Fed treatment contained more ($P<0.05$) CLA *c*-9, *t*-11 than the <90 Day Fed treatment, both containing more ($P<0.05$) CLA than the 50:50 Forage:Grain and Feedlot Finishing treatments (Fig. 3.12.), which were similar ($P>0.05$). Slice separation for treatment differences within the perirenal tissue indicated that the CLA content of the Forage Fed and <90 Day Fed treatments were similar ($P>0.05$), both having a greater ($P<0.05$) CLA content than found in the 50:50 Forage:Grain treatment (Fig. 3.12.). The Feedlot Finishing treatment had a CLA content intermediate ($P>0.05$) between the <90 Day Fed and 50:50 Forage:Grain treatments. Treatment differences within intramuscular tissue show the Forage Fed and <90 Day Fed treatments being similar ($P>0.05$) and the 50:50 Forage:Grain and Feedlot Finishing treatments being similar ($P>0.05$), with the former being greater ($P<0.05$) than the latter (Fig. 3.12.). Slice evaluation for tissues within treatments indicated CLA content to be greatest ($P<0.05$) in subcutaneous tissue as opposed to perirenal or

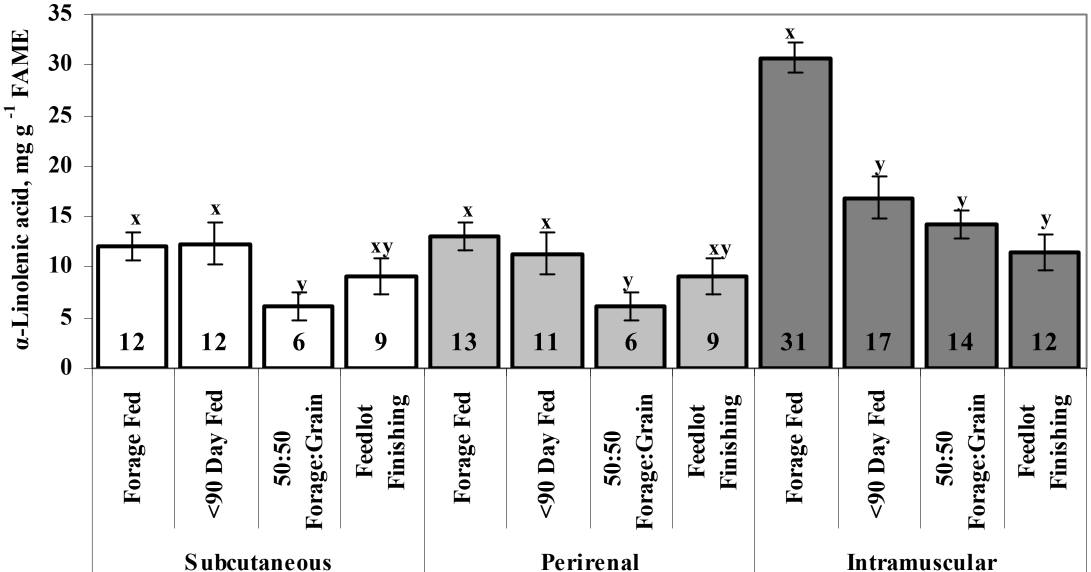

Figure 3.11. Dietary treatment x tissue type interaction for α-linolenic acid (C18:3 *c*-9, 12, 15) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=1.43, <90 Day Fed=2.08, 50:50 Forage:Grain=1.39, Feedlot Finishing=1.80.

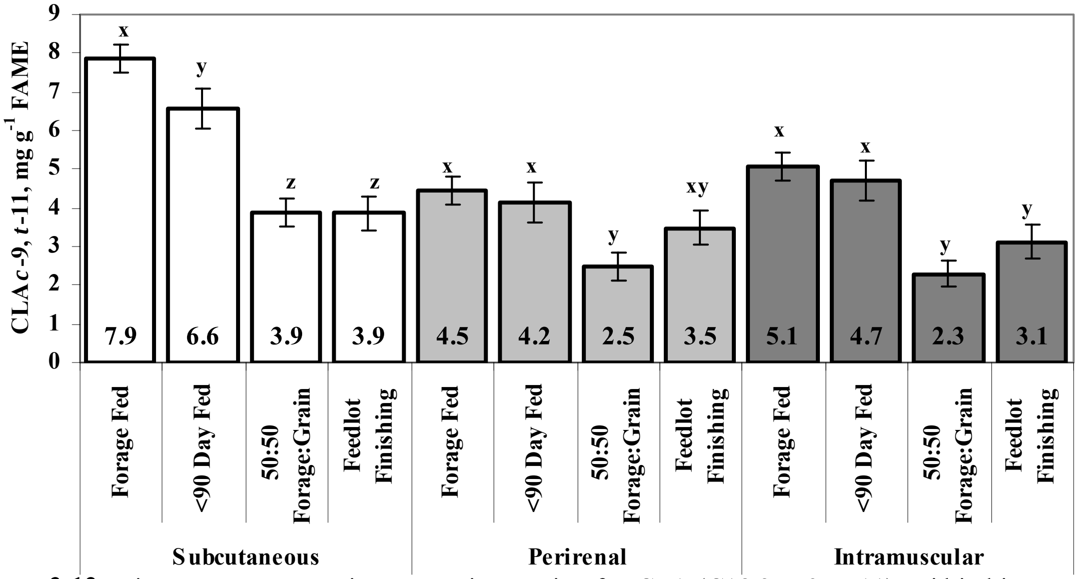

Figure 3.12. Dietary treatment x tissue type interaction for CLA (C18:2 *c*-9, *t*-11) acid in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=0.35, <90 Day Fed=0.51, 50:50 Forage:Grain=0.34, Feedlot Finishing=0.44.

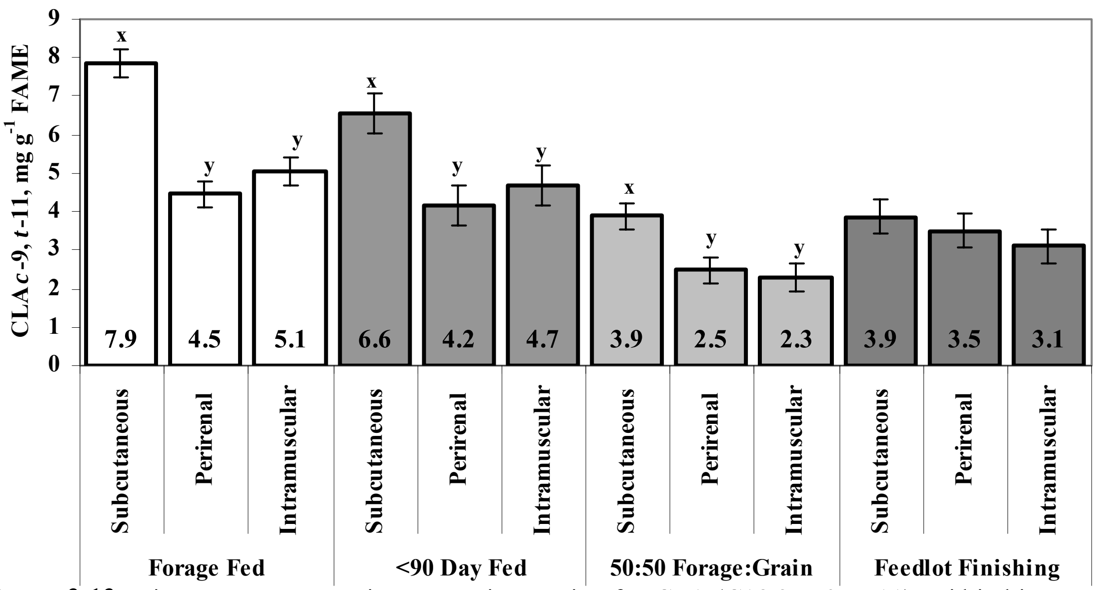

Figure 3.13. Dietary treatment x tissue type interaction for CLA (C18:2 *c*-9, *t*-11) acid in bison, means separation for tissue type within dietary treatment. Means within treatment followed by different letters (x,y,z) are different (P<0.05). Pooled SEM for Forage Fed=0.35, <90 Day Fed=0.51, 50:50 Forage:Grain=0.34, Feedlot Finishing=0.44.

intramuscular tissue which were similar (*P*>0.05) for all treatments (Fig. 3.13.), except Feedlot Finishing where all tissues were equivalent (*P*>0.05). Although trace amounts of the 18:2 *t*-10, *c*-12 isomer of CLA was identified, variances within tissues and treatments were not significant (*P*>0.05).

Minor C18 Polyunsaturated Fatty Acids

Only minor amounts of γ-linolenic acid were identified in the tissues, with the effect (*P*<0.05) of tissue indicating the majority (*P*<0.05) of γ-linolenic acid accumulated in the intramuscular tissue (Table 3.1.). Effect (*P*<0.05) of treatment indicate the Forage Fed and 50:50 Forage:Grain treatments to be similar (*P*<0.05) and the <90 Day Fed and Feedlot Finishing treatments to be similar (*P*<0.05), with the former pair being higher (*P*<0.05) than the latter pair.

3.3.4. Saturated and Unsaturated Fatty Acids of C20 to C22 Chain Length

20:4 Arachidonic

There was an interaction (*P*<0.05) between treatments and tissue types for arachidonic acid (Table 3.2.). Separation of simple effects (*P*<0.05) of treatment within intramuscular tissue showed the Forage Fed and 50:50 Forage:Grain treatments were similar (*P*>0.05), and both had a greater (*P*<0.05) amount of arachidonic acid than the <90 Day Fed or Feedlot Finishing groups, which were similar (*P*>0.05) (Fig. 3.14.). Simple effects (*P*<0.05) of tissue within all treatments indicated intramuscular tissue containing more (*P*<0.05) arachidonic acid than subcutaneous or perirenal tissue, which were similar (*P*>0.05).

20:5 Eicosapentaenoic

An interaction (*P*<0.05) between treatments and tissue types was identified for eicosapentaenoic acid (Table 3.2.). Separation of simple effects (*P*<0.05) within intramuscular tissue showed the Forage Fed treatment contained the greatest (*P*<0.05) amount of eicosapentaenoic acid, followed by the 50:50 Forage:Grain with the Forage Fed and Feedlot Finishing treatments being comparable (*P*>0.05) and with the least (*P*<0.05) amount of eicosapentaenoic acid (Fig. 3.15.). Separation of simple

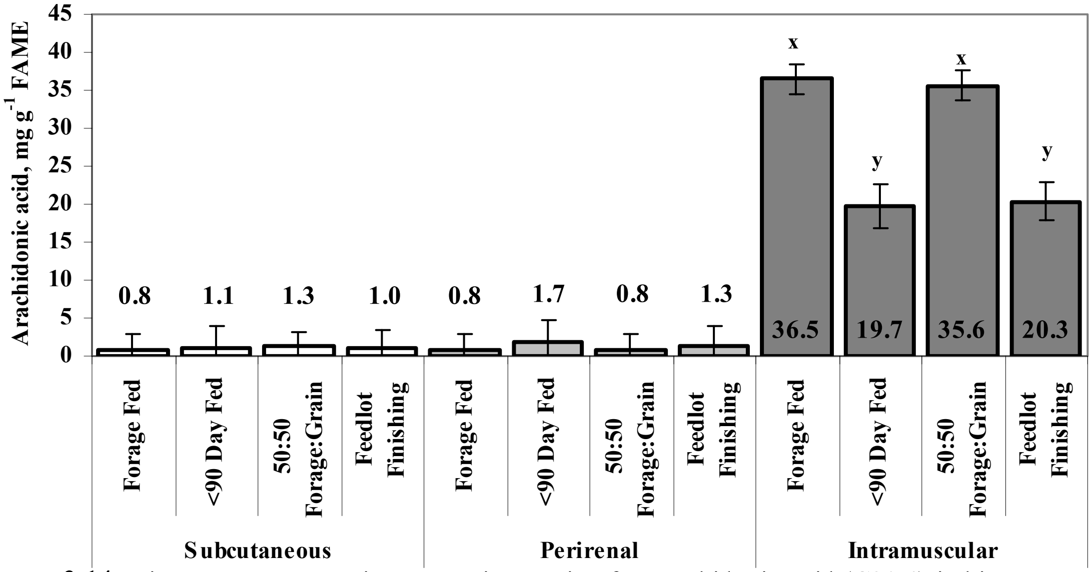

Figure 3.14. Dietary treatment x tissue type interaction for arachidonic acid (C20:4) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=2.00, <90 Day Fed=2.91, 50:50 Forage:Grain=1.95, Feedlot Finishing=2.52.

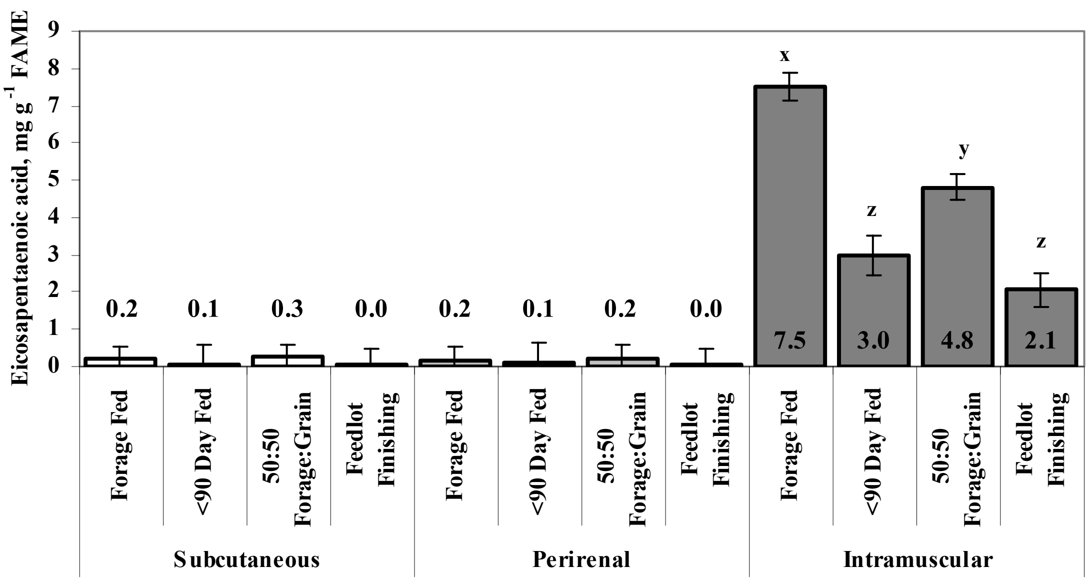

Figure 3.15. Dietary treatment x tissue type interaction for eicosapentaenoic acid (C20:5) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=0.36, <90 Day Fed=0.53, 50:50 Forage:Grain=0.35, Feedlot Finishing=0.46.

effects (P<0.05) for tissue within all treatments showed more (P<0.05) eicosapentaenoic acid was detected in the intramuscular tissue compared to the subcutaneous or perirenal content, which were comparable (P>0.05).

22:5 Docosapentaenoic

There was an interaction effect (P<0.05) between treatments and tissue types for docosapentaenoic acid (Table 3.2.). Within intramuscular tissue, the Forage Fed treatment contained the greatest (P<0.05) amount of docosapentaenoic acid, followed by the 50:50 Forage:Grain treatment, with the Feedlot Finishing treatment having the least (P<0.05) amount of docosapentaenoic acid (Fig. 3.16.). The <90 Day Fed treatment was intermediate (P>0.05) between the 50:50 Forage:Grain and Feedlot Finishing treatment (Fig. 3.16.). Docosapentaenoic acid content was greater (P<0.05) in the intramuscular tissue than in the subcutaneous or perirenal tissue across all treatments.

22:6 Docosahexaenoic

An interaction effect (P<0.05) between treatments within tissue types was identified for docosahexaenoic acid content (Table 3.2.). Simple effects (P<0.05) indicate that within intramuscular tissue, the Forage Fed treatment contained more (P<0.05) docosahexaenoic acid that the other three treatments. The 50:50 Forage:Grain treatment contained more (P<0.05) docosahexaenoic acid than the Feedlot Finishing treatment, with the <90 Day Fed treatment being similar (P>0.05) to both (Fig. 3.17.). Simple effects (P<0.05) of tissues within treatments for docosahexaenoic acid content indicate a greater (P<0.05) amount in the intramuscular tissue than in the subcutaneous or perirenal tissue across all treatments.

Minor C20 to C22 Fatty Acids

Minor saturated fatty acids identified in the C20:0 to C22:0 range of fatty acids include arachidic and behenic acid. An interaction (P<0.05) between treatments and tissue types was identified for arachidic acid (Table 3.2.). Simple effects (P<0.05) indicate that within the subcutaneous and perirenal tissues, the 50:50 Forage:Grain

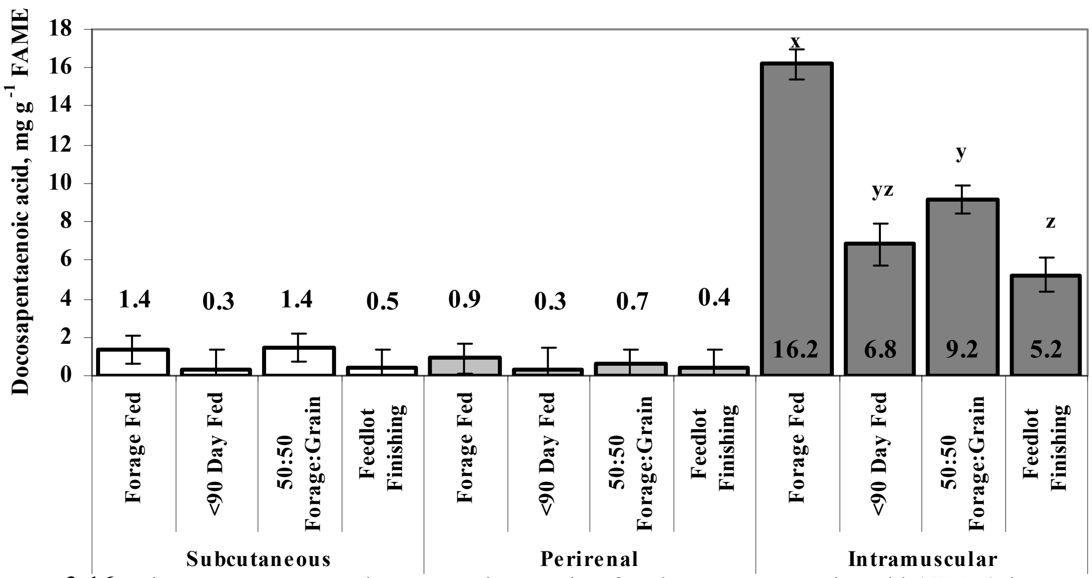

Figure 3.16. Dietary treatment x tissue type interaction for docosapentaenoic acid (C22:5) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=0.74, <90 Day Fed=1.07, 50:50 Forage:Grain=0.72, Feedlot Finishing=0.93.

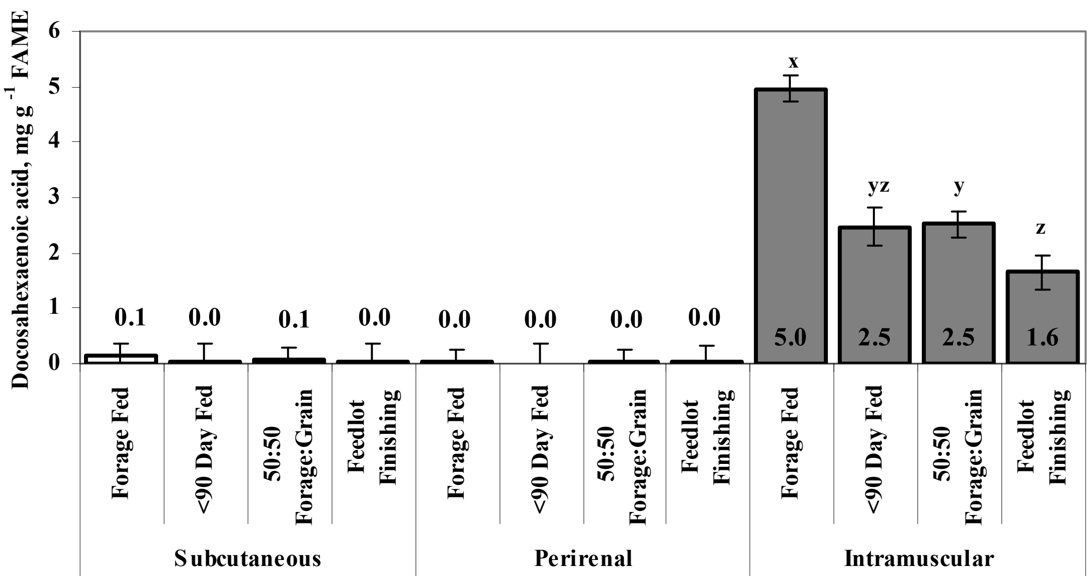

Figure 3.17. Dietary treatment x tissue type interaction for docosahexaenoic acid (C22:6) in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=0.24, <90 Day Fed=0.35, 50:50 Forage:Grain=0.23, Feedlot Finishing=0.30.

treatment contained greater (P<0.05) amounts of arachidic acid than the other three treatments, which were similar (P>0.05). Simple effects (P<0.05) for tissue differences within treatments show that perirenal tissue contains more (P<0.05) arachidic acid than subcutaneous or intramuscular tissue in both the Forage Fed and Feedlot Finishing treatments. Within the 50:50 Forage:Grain treatment, perirenal contained the greatest (P<0.05) amount, followed by the subcutaneous, with the intramuscular tissue having the least (P<0.05). The only detectable levels of behenic acid found within treatments, indicated more (P<0.05) behenic acid was found in the subcutaneous and perirenal tissue than in the intramuscular tissue for both Forage Fed and the <90 Day Fed treatment (Table 3.2.).

Minor monounsaturated fatty acids identified in the C20:0 to C22:0 range of fatty acids include: eicosenoic and erucic acid. There was an interaction (P<0.05) for eicosenoic acid (Table 3.2.). Simple effects (P<0.05) showed that within subcutaneous tissue, the Forage Fed treatment contained more (P<0.05) than the other three treatments. In the Forage Fed treatment, subcutaneous tissue contained greater (P<0.05) amounts of eicosenoic acid than the other tissues, which were similar (P>0.05). In the 50:50 Forage:Grain treatment, intramuscular tissue contained more (P<0.05) eicosenoic acid than the other tissues, which were similar (P>0.05).

There was an interaction (P<0.05) between treatment and tissue types for erucic acid (Table 3.2.). Simple effects (P<0.05) showed that within intramuscular tissue, the Forage Fed and <90 Day Fed treatments were similar (P>0.05) and the 50:50 Forage:Grain and Feedlot Finishing treatments were similar (P>0.05), with the former containing greater (P<0.05) amounts of erucic acid than the latter. Simple effects (P<0.05) within treatments indicated intramuscular tissue contained more (P<0.05) erucic acid than the subcutaneous or perirenal tissue in both the Forage Fed and 50:50 Forage:Grain treatments. In the Feedlot Finishing treatment, erucic acid levels were higher (P<0.05) in the intramuscular tissue than in perirenal tissue, with subcutaneous tissue being intermediate (P>0.05).

Minor polyunsaturated fatty acids identified in the C20:0 to C22:0 range of fatty acids include: eicosadienoic, homo-γ-linolenic, eicosatrienoic, docosadienoic and docosatetraenoic acid. For all the minor PUFA's identified, there was more ($P<0.05$) located in the intramuscular tissue than in either subcutaneous or perirenal tissue.

There was an interaction effect ($P<0.05$) between treatments and tissue types for eicosadienoic acid (Table 3.2.). Simple effects ($P<0.05$) within intramuscular tissue showed the content of eicosadienoic acid in the Forage Fed, <90 Day Fed and 50:50 Forage:Grain treatments were similar ($P>0.05$), all treatments having greater ($P<0.05$) amounts than found in the Feedlot Finishing treatment.

Effects ($P<0.05$) for treatment for homo-γ-linolenic acid indicated the greatest ($P<0.05$) amount was in the 50:50 Forage:Grain treatment (Table 3.1.). The Forage Fed treatment contained more ($P<0.05$) homo-γ-linolenic than the Feedlot Finishing treatment, with the <90 Day Fed treatment being intermediate ($P>0.05$). Effects ($P<0.05$) for tissue types indicate a greater ($P<0.05$) proportion in intramuscular than in either subcutaneous or perirenal tissue.

Tissue type effects ($P<0.05$) indicate a greater ($P<0.05$) content of eicosatrienoic acid in intramuscular tissue compared to subcutaneous or perirenal tissue (Table 3.1.).

Effects ($P<0.05$) of treatment for docosadienoic acid show the largest ($P<0.05$) amount to be in the 50:50 Forage:Grain treatment and the least in the Feedlot Finishing treatment (Table 3.1.). More ($P<0.05$) docosadienoic acid was found in the 50:50 Forage:Grain treatment than in the <90 Day Fed treatment, with the Forage Fed treatment intermediate to the two. There was more ($P<0.05$) docosadienoic acid in the Forage Fed treatment than in the Feedlot Finishing treatment, with the <90 Day Fed treatment being intermediate. Tissue effects indicate a greater ($P<0.05$) proportion of docosadienoic acid located in intramuscular tissue than in either subcutaneous or perirenal tissue (Table 3.1.).

Tissue type effects ($P<0.05$) for docosatetraenoic acid showed a greater ($P<0.05$) content in intramuscular tissue than either subcutaneous or perirenal tissues (Table 3.1.).

3.3.5. Fatty Acid Totals and Selected Ratios

An interaction effect (*P*<0.05) between treatment and tissue type for the total saturated fatty acid (SFA) content, measured by percent fatty acid methyl esters are shown in Table 3.4. Within perirenal tissue, simple effects (*P*<0.05) indicate the <90 Day Fed group contained more (*P*<0.05) than the Forage Fed group, with the 50:50 Forage:Grain group being intermediate. All three treatments contained more (*P*<0.05) total saturated fat than the Feedlot Finishing group in perirenal tissue (Fig. 3.18.). Simple effects (*P*<0.05) indicate perirenal tissue had greater levels (*P*<0.05) of total saturated fatty acids than subcutaneous tissue, with intramuscular tissue having the lowest (*P*<0.05).

An interaction effect (*P*<0.05) was identified between treatments and tissue types for the total polyunsaturated fatty acid content (Table 3.4.). Within intramuscular tissue, simple effects (*P*<0.05) showed the Forage Fed and 50:50 Forage:Grain treatments were similar (*P*>0.05), both having a higher (*P*<0.05) content than the <90 Day Fed and Feedlot Finishing treatments (Fig. 3.19.). Within treatments, simple effects (*P*<0.05) indicated intramuscular tissue contained more (*P*<0.05) total polyunsaturated fatty acids (PUFA) than either subcutaneous or perirenal tissue.

There was an interaction (*P*<0.05) between treatments and tissue types for the polyunsaturated to saturated fatty acid ratio. The polyunsaturated to saturated ratio of the Forage Fed treatment was greater than that of the 50:50 Forage:Grain treatment, both having a higher (*P*<0.05) ratio than either the <90 Day Fed or Feedlot Finishing groups (Fig. 3.20.), which were similar (*P*>0.05). Simple effects (*P*<0.05) indicated that within treatments, intramuscular tissue had a higher (*P*<0.05) polyunsaturated to saturated fatty acid ratio than either the subcutaneous or perirenal tissue, which were indistinguishable (*P*>0.05) from each other.

An interaction effect (*P*<0.05) between treatments and tissue types was identified (Table 3.4.) for the total omega-3 content. Simple effects (*P*<0.05) showed within intramuscular tissue, the Forage Fed treatment contained the greatest (*P*<0.05) amount of omega-3 fatty acids, followed by the <90 Day Fed and 50:50 Forage:Grain treatments being similar (*P*>0.05), but containing more (*P*<0.05) omega-3's than the Feedlot Finishing treatment (Fig. 3.21.). Within treatments simple effects (*P*<0.05)

Table 3.3. Main effects for total fatty acid groups of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison fed under four different finishing strategies

	Treatment[z]					Tissue[z]				
	Forage Fed	<90 Day Fed	50:50 Forage:Grain	Feedlot Finishing	P SEM	Subcutaneous	Perirenal	Intramuscular	P SEM	Effect
	mg g^{-1} total fatty acid methyl esters									
SFA	521.53	545.26	535.75	513.15	5.72	538.86	644.00	403.91	5.65	*c*
PUFA	100.37	81.83	88.22	67.06	6.14	41.01	37.95	174.14	6.06	*c*
PUFA/SFA[z]	0.23	0.18	0.20	0.15	0.02	0.08	0.06	0.44	0.02	*c*
ω-3[x]	29.28	17.97	15.42	13.38	1.56	11.08	10.69	35.28	1.54	*c*
ω-6[y]	83.09	71.79	77.75	59.72	5.50	34.02	33.18	152.06	5.42	*c*
ω-6/ω-3	2.73 f	4.02 e	5.00 d	4.35 de	0.29	3.53 e	3.51 e	5.03 d	0.29	*ab*

a-b , means within main effect differ (P <0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (P <0.05), shown on Table 3.4.

d-f, means within a row are different (P <0.05) for each main effect.

[z] sample numbers for Forage Fed subcutaneous, perirenal, and intramuscular tissue, n=12; <90 Day subcutaneous, perirenal, and intramuscular tissue, n=9; 50:50 Forage:Grain subcutaneous, perirenal, and intramuscular tissue, n=20; Feedlot Finishing subcutaneous, perirenal, and intramuscular tissue, n=12.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-3 fatty acids include 18:3 *cis* -9,12,15, 20:3 *cis* -11,14,17, 20:5 *cis* -5,8,11,14,17, 22:5 *cis* -7,10,13,16,19, 22:6 *cis* -4,7,10,13,16,19.

[w] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 *cis* -5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

Table 3.4. Interaction effects (*P* <0.05) for total fatty acid groups of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison fed under four different finishing strategies

	Forage Fed[z]			<90 Day Fed[z]			50:50 Forage:Grain[z]			Feedlot Finishing[z]			
	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
	mg g^{-1} total fatty acid methyl esters												
SFA	526.65	638.20	401.18	553.93	684.52	397.84	538.27	659.93	410.89	537.84	594.07	407.44	10.46
PUFA	40.91	38.50	221.69	45.81	44.90	154.77	39.01	29.69	195.96	38.32	38.71	124.16	11.22
PUFA/SFA[z]	0.08	0.06	0.55	0.08	0.07	0.39	0.07	0.04	0.48	0.07	0.07	0.30	0.03
ω-3[x]	13.82	14.22	59.80	12.71	11.83	29.37	8.02	7.04	31.21	9.77	9.65	20.73	2.85
ω-6[y]	18.97	19.57	155.73	26.48	28.61	120.31	26.60	19.78	161.42	24.56	25.45	99.99	10.05

[z] sample numbers for Forage Fed subcutaneous, perirenal, and intramuscular tissue, n=12; <90 Day subcutaneous, perirenal, and intramuscular tissue, n=9; 50:50 Forage:Grain subcutaneous, perirenal, and intramuscular tissue, n=20; Feedlot Finishing subcutaneous, perirenal, and intramuscular tissue, n=12.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-3 fatty acids include 18:3 *cis* -9,12,15, 20:3 *cis* -11,14,17, 20:5 *cis* -5,8,11,14,17, 22:5 *cis* -7,10,13,16,19, 22:6 *cis* -4,7,10,13,16,19.

[w] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 *cis* -5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

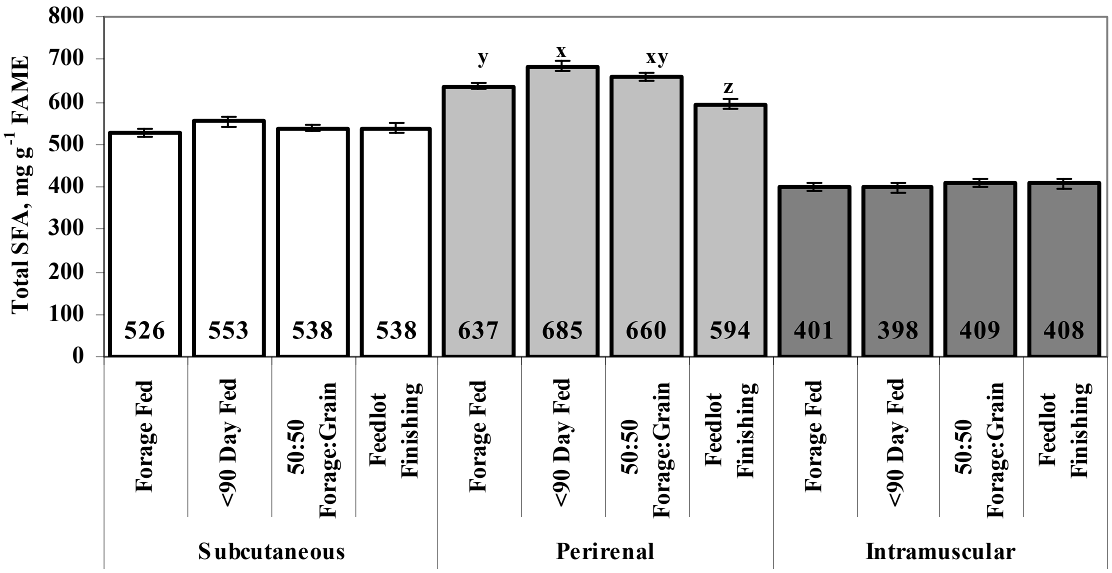

Figure 3.18. Dietary treatment x tissue type interaction for total saturated fatty acids in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=8.81, <90 Day Fed=12.79, 50:50 Forage:Grain=8.58, Feedlot Finishing=11.08.

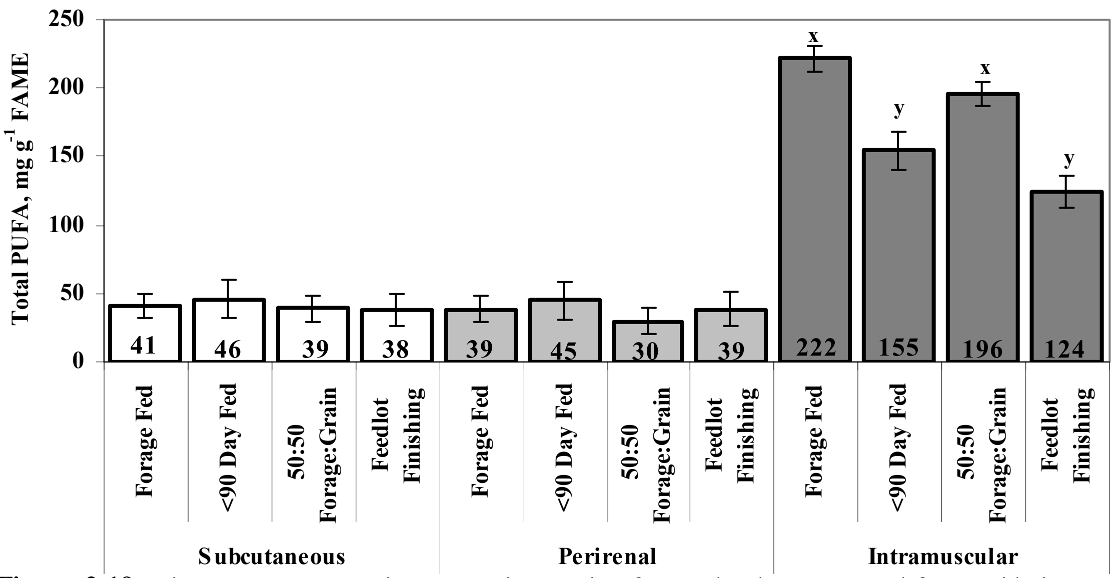

Figure 3.19. Dietary treatment x tissue type interaction for total polyunsaturated fatty acids in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=9.45, <90 Day Fed=13.73, 50:50 Forage:Grain=9.21, Feedlot Finishing=11.89.

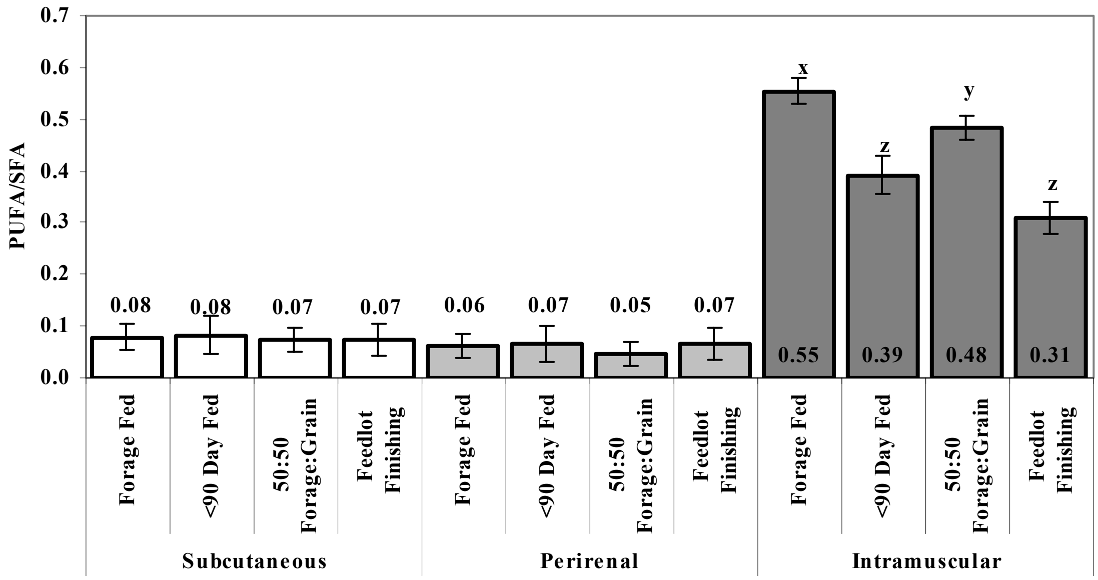

Figure 3.20. Dietary treatment x tissue type interaction for the ratio of polyunsaturated to saturated acids in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=0.02, <90 Day Fed=0.04, 50:50 Forage:Grain=0.02, Feedlot Finishing=0.03.

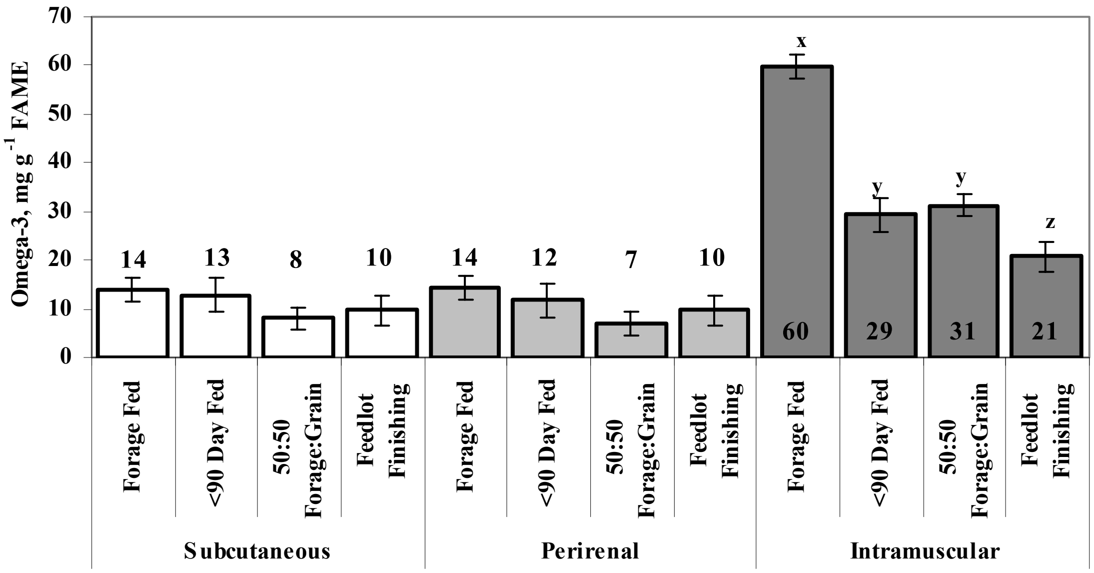

Figure 3.21. Dietary treatment x tissue type interaction for the total omega-3 fatty acids in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=2.40, <90 Day Fed=3.49, 50:50 Forage:Grain=2.34, Feedlot Finishing=3.02.

indicated that intramuscular tissue contained more (*P*<0.05) omega-3 fatty acids than subcutaneous or perirenal tissue.

Interaction (*P*<0.05) between treatments and tissue types for total omega-6 fatty acid content was apparent (Table 3.4.). Within intramuscular tissue, simple effects (*P*<0.05) indicate the omega-6 fatty acid content was similar (*P*>0.05) between the Forage Fed and 50:50 Forage:Grain treatments, both having a greater (*P*<0.05) omega-6 fatty acid content than either the <90 Day Fed or Feedlot Finishing treatments, which were similar (*P*>0.05), (Fig. 3.22.). Separation of simple effects (*P*<0.05) across all treatments indicated intramuscular tissue contained more (*P*<0.05) omega-6 fatty acids than subcutaneous or perirenal tissue.

Effects (*P*<0.05) for the ratio of omega-6 to omega-3 fatty acids are given in Table 3.3. Effect (*P*<0.05) of tissue for the omega-6 to omega-3 ratio were higher (*P*<0.05) in intramuscular tissue than in subcutaneous or perirenal tissue (Table 3.3.). Effect (*P*<0.05) of treatment indicated that the 50:50 Forage:Grain treatment had the highest (*P*<0.05) omega-6 to omega-3 ratio (5.0), followed by the <90 Day Fed treatment (4.0), with the Feedlot Finishing treatment (4.3) being intermediate (*P*>0.05), (Fig 3.23.). The Forage Fed treatment (2.7) had the lowest (*P*<0.05) omega-6 to omega-3 ratio compared to the other three treatments (Fig. 3.23.).

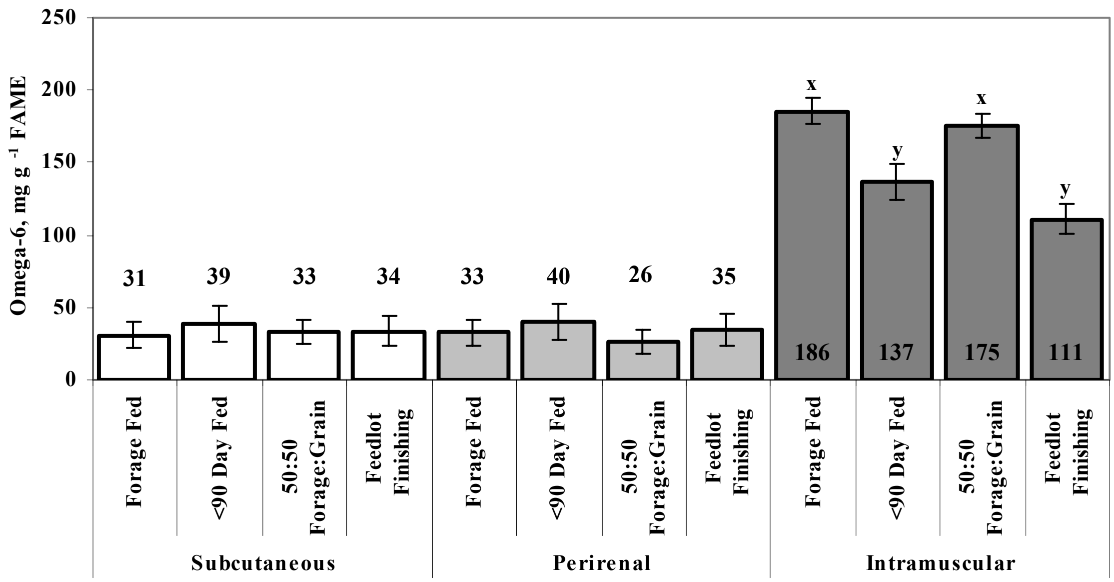

Figure 3.22. Dietary treatment x tissue type interaction for the total omega-6 fatty acids in bison, means separation for dietary treatment within tissue type. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for Forage Fed=8.46, <90 Day Fed=12.29, 50:50 Forage:Grain=8.25, Feedlot Finishing=10.65.

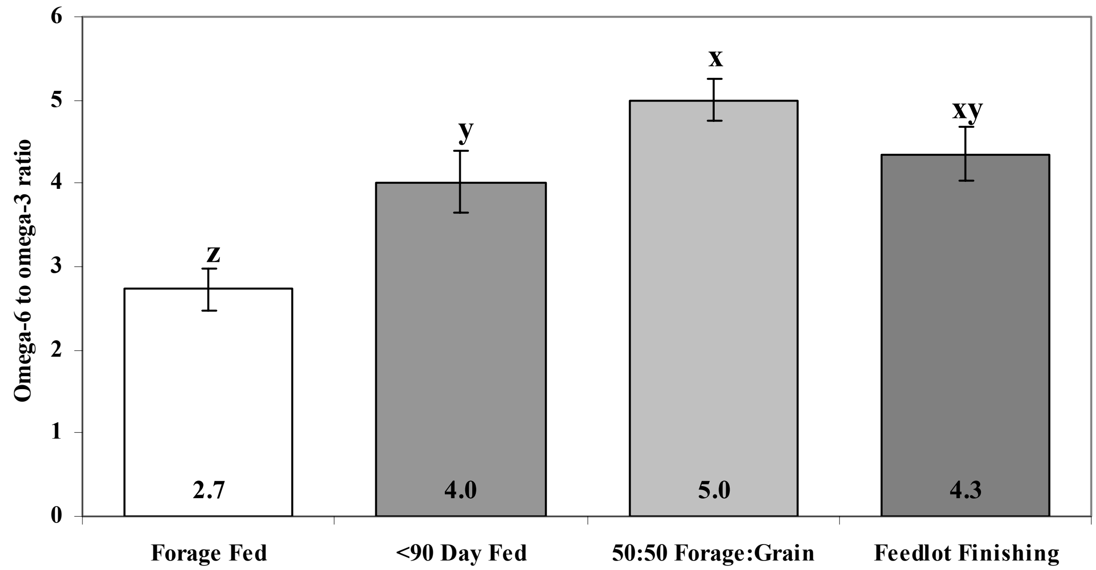

Figure 3.23. Effect of treatment for the ratio of omega-6 to omega-3 fatty acids in bison. Means followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for Forage Fed=0.26, <90 Day Fed=0.37, 50:50 Forage:Grain=0.25, Feedlot Finishing=0.32.

3.4. Discussion

The samples collected from animals within this study were typical of those found under commercial conditions, and would be representative of the bison industry within Saskatchewan. Commercial producers representing each of the four feeding programs supplied the tissue samples for this study. Factors such as ration composition, time of slaughter, and age of animal at the time of slaughter were all decisions made by the individual producer making feed intake and nutrient composition of the diet impossible to control or record. Information gathered during the study provides a one time look at the fatty acid profile of bison tissues produced under commercial conditions.

The highest proportion of total saturated fatty acids in bison was found in the perirenal tissue, followed by the subcutaneous, then intramuscular tissue (Table 3.4.). These findings are in agreement with the findings of Marmer et al. (1984) and Bolte et al. (2002) where the subcutaneous adipose deposits tended to be less saturated than those of the body core. The saturation of subcutaneous tissue has also been noted in relation to seasonal effects where by tissue becomes less saturated as temperature decreases (Tume et al. 2004). The change in saturation level of the subcutaneous tissue results in a shift towards monounsaturated fatty acids and has been related to Δ-9 desaturase activity within the tissues (Link et al. 1970). Higher proportions of unsaturated fatty acids within the tissue would lower the melting point, aiding in tissue fluidity and metabolic function. Differences amongst saturated fatty acids and the tissues show that there was about half the myristic acid located within the intramuscular tissue than found in either the subcutaneous or perirenal tissue. Between tissues, palmitic acid content found in intramuscular tissue was roughly 80% of that found in subcutaneous or perirenal tissue. Stearic acid content of the tissues showed the greatest variability, with perirenal tissue having the greatest proportion, and subcutaneous and intramuscular tissue respectively containing 70% and 40% of that of perirenal tissue.

Treatment effects within perirenal tissue indicated lower saturation for feedlot fed bison. High concentrate diets have been shown to produce higher concentrations of oleic acid at the expense of stearic acid (Wood et al. 2003). Forage diets tend to be high in linolenic and linoleic acid, both of which undergo almost complete biohydrogenation in the rumen, lending to increased amounts of stearic acid incorporated into the tissue. A high forage diet during most of the finishing period, followed by a short, high-energy feeding period prior to slaughter, would promote the formation of stearic followed by enrichment of the tissue with palmitic acid. As more fatty acids are synthesized, as found on a higher concentrate ration, there is an associated increase in elongation and desaturation activity (St. John et al. 1991). Fatty acid elongation activity has been found to be three times higher than desaturase activity within subcutaneous adipose tissue (St. John et al. 1991).

Forage fed ruminants have higher proportions of pentadecanoic acid and less margaric acid than animals fed on high concentrate rations, as cited by Larick and Turner (1989). Marchello et al. (1998) found feedlot fed bison to have a greater proportion of pentadecanoic than margaric acid. In agreement with the findings of Marchello and Driskell (2001), animals fed forage up to slaughter contained a greater proportion of pentadecanoic and margaric acid compared to animals finished on high concentrate diets. Rule et al. (2002) found forage fed bison to have more pentadecanoic than margaric acid in intramuscular tissue, whereas in feedlot bison there was a slightly greater amount of margaric than pentadecanoic acid, which is in agreement with the findings of this study.

Although greater amounts of total saturated fatty acids were found in muscle tissue from forage than form feedlot finished bison by both Rule et al. (2002) and Marchello and Driskell (2001), there were no differences between feeding treatments for myristic or palmitic acid content. Within this study, the total amount of saturated fatty acids was similar across all treatment groups within intramuscular tissue. Of the saturated fatty acids within intramuscular tissue, stearic acid content was similar across treatments. However, Rule et al. (2002) found greater proportions of stearic acid within the tissue of forage fed animals. While total saturated fatty acid content of intramuscular tissue is unaffected by treatment, both myristic and palmitic content are affected. Myristic acid content was slightly greater within the Feedlot Finishing treatment. Palmitic acid had the greatest variability between treatments, with greater proportions being found in animals on a high concentrate diet at the time of slaughter rather than on a mainly forage based diet as found in the Forage Fed and 50:50 Forage:Grain animals, which was similar to the findings of Rule et al. (2002).

Consumption of saturated fatty acids synthesized within the rumen, such as lauric, myristic, and especially the hypercholesterolemic fatty acid, palmitic acid, have all been associated with increased risk of coronary heart disease in humans (Welch and Borlakoglu 2000; St. John et al. 1991). Although stearic acid makes up a large portion of the saturated fatty acids found in ruminant tissue, it has not been shown to have any cholesterolemic effects (Rhee 2000).

Short term high concentrate feeding raised the oleic acid content of the intramuscular tissue in the <90 Day treatmentto the equivalent of that of Feedlot intramuscular tissue, while the Forage Fed and 50:50 Forage:Grain treatments were similar but had only 80% of the oleic content of the former treatments. Intake of grain while on pasture for bison in the 50:50 Forage:Grain treatment was not sufficient to increase the oleic content of the intramuscular tissue. Oleic acid is the predominant *cis*-monounsaturated fatty acid found in ruminant tissue. Increased rates of fatty acid synthesis, as found with high energy diets, have been associated with increased rates of fatty acid elongation and desaturation within tissues (St. John et al. 1991). Compared to high forage diets, high concentrate diets lend more to the deposition of oleic acid than stearic acid within muscle tissue (Loor et al. 2003; Larick and Turner 1989; Daniel et al. 2004). Similar effects of short term grain feeding have been noted by Duckett et al. (1993) and Griswold et al. (2003), while the reverse effects have been noted by Noci et al. (2005) when animals where switched from a high concentrate diet to short term forage finishing.

Treatment effects for *trans*vaccenic acid content were limited to subcutaneous and perirenal tissue, with roughly twice as much found in the Forage Fed treatment relative to the other treatments for both tissues. Although *trans*vaccenic acid content of the intramuscular tissue was similar across treatments, comparisons showed Forage Fed intramuscular tissue to contain 30% of the *trans*vaccenic acid found in subcutaneous tissue, whereas in the Feedlot Finishing treatment, intramuscular tissue had 40% of the *trans*vaccenic acid found in subcutaneous tissue. Formation of *trans*vaccenic acid within the rumen is the rate-limiting step during the biohydrogenation of both linoleic and linolenic acid. Subsequent accumulation and passage results in the incorporation of greater amounts of *trans*vaccenic acid into tissues. Intake of monounsaturated *trans* fatty acids has been linked to increased low-density lipoprotein and serum cholesterol levels while lowering high-density lipoprotein concentrations in the blood (Bauman et al. 2004). Studies into the detrimental effects of *trans*-fatty acids in human health have focused on those derived from partially hydrogenated vegetable oils, in particularly elaidic acid and its link to coronary heart disease. Hodgson et al. (1996) as cited by Bauman et al. (2004), reported a positive association between the consumption of partially hydrogenated vegetable oil containing both *trans*-9 and *trans*-10 C18:1 and the risk of coronary heart disease, while no such link has been made to *trans*-vaccenic acid. Although mono-*trans*-octadecenoic fatty acids are only present in minor amounts in ruminant tissue, the majority being in the form of *trans*-11 vaccenic acid, there is a negative association between the mono-*trans*-octadecenoic acids of animal origin and the risk of coronary heart disease (Bauman et al. 2004).

Total polyunsaturated fatty acid content of the intramuscular tissue was greater in both the Forage Fed and 50:50 Forage:Grain treatments, where forage was fed up to the time of slaughter (Table 3.4.). The total polyunsaturated fatty acid content in the Feedlot Finishing treatment was 44% of that found in the Forage Fed treatment. Polyunsaturated fatty acids are of dietary origin and derived from either linoleic or linolenic acid. Polyunsaturated fatty acids are most often associated with phospholipids due to specificity of the acyl-transferase. The majority of lipid cells in the subcutaneous and perirenal adipose tissue are comprised of saturated or monounsaturated triacylglycerides with small amounts of polyunsaturated fatty acids associated with surrounding phospholipid membranes. Linoleic, α-linolenic and arachidonic acid content accounted for the majority of differences between treatments for polyunsaturated fatty acid content within intramuscular tissue (Table 3.2.).

The majority of the lipid found in cereal and most oilseeds is linoleic acid (Becker 2000). Linoleic acid content of intramuscular tissue varied mostly with the amount of forage in the diet and period in which it was fed. The highest concentrations of linoleic acid were found in the 50:50 Forage:Grain treatment, possibly due to greater combined intake of linoleic acid resulting in less lipolysis or biohydrogenation within the rumen. Less biohydrogenation and shorter rumen retention time could be a result of the faster digestion rate of cereal grains and a resulting decrease in rumen pH. The galactolipids associated with plant tissue are less rapidly hydrolysed than the triglycerides associated with cereal grains, potentially allowing more longer-chain fatty acids to escape biohydrogenation (Harfoot and Hazlewood 1997). The Feedlot Finishing treatment had 65% of the linoleic acid content of the 50:50 Forage:Grain treatment for the linoleic acid content of the intramuscular tissue. The lower content found in the Feedlot Finishing treatment could be due to a number of factors affecting ruminal pH, biohydrogenation, or absorption or subsequent dilution of fatty acids by monounsaturated derivatives. Regardless of possible scenarios, lesser amounts of linoleic acid were found within the Feedlot Fed and <90 Day Fed treatments, but with greater amounts of oleic acid within the intramuscular tissue, without any differences in the stearic acid content of the tissue as would be expected from a high concentrate diet. Although no significant effect of short term grain feeding was found, indications were noted to be similar to that of Duckett et al. (1993), where linoleic content of tissue was affected by grain feeding period.

Forage lipids consist primarily of α-linolenic with lesser amount of linoleic acid (Elgersma et al. 2003). Similar to the findings of Rule et al. (2002), Forage Fed animals had the greatest content of α-linolenic acid within intramuscular tissue. Treatment differences within intramuscular tissue show the Forage Fed treatment to have 45% more α-linolenic acid content than the other treatments, but within subcutaneous and perirenal tissue, only the 50:50 Forage:Grain treatment was different, containing roughly half the α-linolenic acid of the Forage Fed or <90 Day Fed treatments. Effects of treatment for the <90 Day Fed group were similar to those of Duckett et al. (1993), in that once animals were removed from pasture, α-linolenic content of the intramuscular tissue was quickly diminished. Like French et al. (2000), animals fed a 50/50 mix of grass and concentrates had α-linolenic content significantly less than that of forage fed animals. Feedlot finishing diets generally result in the lowest tissue content of α-linolenic acid, as found in this study. Beef related studies have shown that the inclusion of linseed oil within a high grain diet appears to be the most effective way of increasing α-linolenic content of ruminant tissues (Scollan et al. 2001b).

Content of CLA was greater in subcutaneous tissue of bison than in either perirenal or intramuscular tissue. A greater amount of CLA in subcutaneous tissue was found in treatments that were fed forage through out the finishing phase; slightly lesser amounts were found in the <90 Day Fed treatment. The CLA content of the subcutaneous tissue of the 50:50 Forage:Grain and Feedlot Finishing treatments was 50% and 60% of the Forage Fed and <90 Day Fed treatments, respectively. Ruminant products are considered to be rich sources of CLA. The CLA content of the intramuscular tissue of the Forage Fed and <90 Day Fed treatments was 66% or more than that found in the 50:50 Forage:Grain or Feedlot Finishing treatments. Potential health benefits attributed to CLA are numerous (Griinari and Bauman 1999). The conjugated linoleic acid isomer *c*-9, *t*-11 is the most common CLA isomer found in ruminant tissues. Conjugated linoleic acid is derived from the desaturation of *t*-11 *trans*vaccenic acid within the tissues by the action of the stearoyl-CoA desaturase enzyme. Reduction in CLA content of milk has been noted when diet changes from primarily forage to concentrate/conserved forage diet (Elgersma et al. 2004, Precht and Molkentin, 2000); similar effects would be expected in muscle tissue as noted in this study. Muscle tissue CLA content has been increased by switching animals from a high concentrate diet to a short-term forage diet (Noci et al. 2005). Treatments that were fed concentrates throughout the finishing phase had the lowest content of CLA within the tissue.

The ratio of polyunsaturated to saturated fatty acids between bison treatments indicate a relationship between the amount of forage fed at the end of the finishing period as well as the overall amount of forage fed during the finishing period. As there were no differences between treatments for the total saturated fatty acid content of intramuscular tissue, differences are noted in relation to the polyunsaturated fatty acid content of the tissue. The Forage Fed treatment contained the greatest proportion of polyunsaturated acids, owing to the greater proportion of α-linolenic and linoleic acid and respective elongase/desaturase derivatives within the intramuscular tissue. The proportion of polyunsaturated fatty acids found in the 50:50 Forage:Grain treatment was similar to that of the Forage Fed treatment, but a greater proportion of oleic acid along with lesser proportions of linolenic acid within the tissue contributed to the slight difference observed in the PUFA to SFA ratio. Short term grain feeding as found with the <90 Day Fed treatment was sufficient to lower the PUFA to SFA ratio to that of the Feedlot Finished treatment. Similar effects were observed by Duckett et al. (1993), where monounsaturated fatty acid content increased at the expense of the polyunsaturated fatty acid content during short-term concentrate feeding. The dilution of polyunsaturated fatty acids within the muscle tissue, as found by Duckett et al. (1993) is most likely due to the increase in intramuscular marbling that occurs as beef animals approach physiological maturity and begin to deposit more fat and less lean tissue. Usually, this determines the finishing period endpoint of the animal. The difference in magnitude between the PUFA to SFA ratio between intramuscular to subcutaneous tissues in Forage Fed bison was almost seven fold, whereas the difference in the Feedlot Finishing treatment for the same tissues was just under 4.5-fold.

Intramuscular tissue contains the greatest proportion of linoleic acid due to its association with the membrane phospholipids. Greater content of linoleic acid within the intramuscular tissue of the Forage Fed and 50:50 Forage:Grain treatments could indicate both a greater intake, and, subsequently more escaping biohydrogenation within the rumen, allowing for absorption and incorporation into the tissues. Biohydrogenation of linoleic acid is estimated to be in the range of 70-95% (Bauman et al. 2003). Lower levels of biohydrogenation have been reported for forage lipids, indicating an interaction with plant tissue, allowing for more polyunsaturated acids to escape the rumen (Doreau and Ferlay 1994). The more polyunsaturated fatty acids in the diet, the greater the depression of biohydrogenation within the rumen (Scollan et al. 2001), thus making more linoleic acid available for absorption. Greater amounts of linoleic acid escaping the rumen will have a subsequent effect on the amount of omega-6 fatty acids, especially arachidonic acid, accumulating in the tissues. Arachidonic acid levels were found to be the highest in the Forage Fed and 50:50 Forage:Grain treatments, 154% greater than in the other treatment. It can be speculated that a greater content of linoleic acid in the diet coupled with incomplete biohydrogenation could be related to these findings. Elongase/desaturase activity of linoleic acid within the muscle tissue results in a greater accumulation of arachidonic acid, which leads to the production of pro-thrombotic and pro-aggregatory eicosanoids characteristic of omega-6 derived eicosanoids, resulting in increased blood viscosity, vasospasm and vasoconstriction, and ultimately decreased bleeding time (Simopoulos 2000).

Within bison treatments, the greater the proportion of dietary forage, the greater the proportion of total omega-3 fatty acids. The Forage Fed treatment contained almost twice the omega-3 content of the <90 Day Fed or 50:50 Forage:Grain treatments, indicating short term high concentrate or long term low concentrate diets significantly affect the accumulation of omega-3 fatty acids. Feedlot Finished bison had the lowest content, with only 35% of the omega-3 fatty acids found in the Forage Fed treatment.

The primary precursor of the omega-3 fatty acid family is α-linolenic acid. Alpha-linolenic acid undergoes almost complete (85-100%) biohydrogenation within the rumen (Bauman et al. 2003). The greater the degree of unsaturation of dietary lipid, such as that of fish oil, the more inhibitory it is to the rumen biohydrogentaion process (Scollan et al. 2001). Potentially the higher the proportion of α-linolenic acid as within a forage-based diet, the greater the amount that will escape the rumen (Moate et al. 2004). Content of α-linolenic within the diet and subsequent incorporation into tissue plays a vital role in the synthesis of long chain omega-3 polyunsaturated fatty acids such as eicosapentaenoic, docosapentaenoic, and docosahexaenoic acid. Elongation/desaturation of linolenic acid within tissue leads to the formation of many fatty acids considered to exhibit beneficial biological functions. Eicosapentaenoic, docosapentaenoic and docosahexaenoic acid all exhibit some function and can be found in substantial quantities naturally in fish oil; lesser amounts can be formed from linolenic acid in mammalian tissues (Kinsella 1990).

Within intramuscular tissue of the bison treatments, Forage Fed animals contained the greatest amount of eicosapentaenoic acid, followed by the 50:50 Forage:Grain treatment having 36% less than Forage Fed; the <90 Day Fed and Feedlot Finished had equivalent contents, but 60% or less of the content found in the Forage Fed treatment. Differences observed between the Forage Fed and 50:50 Forage:Grain treatments might suggest that although grain intake of the 50:50 Forage:Grain treatment was not enough to lower ruminal pH to decrease biohydrogenation, grain intake was sufficient to meet daily caloric intake which decreased forage intake. Short term grain feeding was sufficient to decrease the eicosapentaenoic acid content of the <90 Day Fed treatment to that of the Feedlot Finished treatment, presumably by rapidly turning over the eicosapentaenoic content of the tissue, based on the findings of Duckett et al. (1993) and Noci et al. (2005). The hypolipidemic, antithrombotic and anti-inflammatory effects of omega-3 fatty acids are largely attributed to eicosanoids derived from eicosapentaenoic acid (Simopoulos 2000).

The docosapentaenoic acid content of the intramuscular tissue of Forage Fed bison was highest and the Feedlot Finished treatment the lowest, while the 50:50 Forage:Grain and <90 Day Fed treatments were intermediate, being greater and similar to the Feedlot Finishing treatment, respectively. Compared to the Forage Fed treatment, the other three treatments had 57% or less of the docosapentaenoic acid content within intramuscular tissue. Docosapentaenoic acid is an elongation product of eicosapentaenoic acid. However, Akiba et al. (2000) found it to be a more potent inhibitor of blood platelet aggregation compared to its precursor, eicosapentaenoic acid or its successor, docosahexaenoic acid.

Differences in docosahexaenoic acid content between treatments were similar to those of docosapentaenoic acid, with the greatest amounts found in Forage Fed, being twice that of either the <90 Day Fed or 50:50 Forage:Grain, and the least in Feedlot Finished treatments, having only 32% of that of the Forage Fed treatment. The difference in magnitude between tissues for docosahexaenoic acid ranged from sixteen times in the Feedlot Finishing treatment to fifty times in the Forage Fed treatment. The importance of docosahexaenoic acid in the diet is with respect to early infant neurological development (Uauy et al. 2001), as well as its protective effect against cardiovascular disease (McLeenan et al. 1996).

Forage Fed animals had the lowest omega-6 to omega-3 ratio. Similarly, Rule et al. (2002) found range finished animals to have a more desirable omega-6 to omega-3 ratio compared to feedlot finished animals. Interestingly, although short term grain feeding resulted in a rapid decrease in omega-3 fatty acids, the <90 Day Fed treatment still had a more desirable ratio than the 50:50 Forage:Grain treatment, which had access to grass throughout the finishing phase. The highest ratio was found in the 50:50 Forage:Grain treatment, being almost twice that of the Forage Fed treatment, which most likely was result of a greater incorporation of linoleic acid and subsequent formation of arachidonic acid within the tissue, due to either a drop in ruminal pH causing decreased biohydrogenation or to rapid ruminal passage rate of linoleic acid. The Feedlot Finishing treatment resulted in a ratio similar to that of the <90 Day Fed and 50:50 Forage:Grain treatments. The ratio of omega-6 to omega-3 fatty acids has an effect on the type and proportion of eicosanoids produced within the body, as well as on the effects exhibited by the individual fatty acids associated with each group. Linoleic and α-linolenic acid compete for the same metabolic pathways giving rise to their respective longer chained polyunsaturated derivatives, such that the omega-3 fatty acids have a greater suppressing effect on the omega-6 fatty acids, while the omega-6 fatty acids have a lesser suppressive effect on the omega-3 fatty acids (Chapkin 2000). This results in a preference for the formation of eicosapentaenoic, docosapentaenoic and docosahexaenoic acid. Eicosapentaenoic acid competes with arachidonic acid for prostaglandin and leukotriene synthesis at the cyclooxygenase and lipoxygenase level (Simopoulos 2002). A lower omega-6 to omega-3 ratio would favor the production of the anti-inflammatory eicosanoids derived from eicosapentaenoic acid. Given the dangers associated with a diet that has a high omega-6 to omega-3 ratio (Simopoulos 2000), selecting foods exhibiting a lower ratio would potentially be beneficial to human health.

3.5. Summary and Conclusions

Although economic and environmental factors may ultimately determine preferred bison finishing practices, preliminary conclusions drawn from this study include:

- Perirenal tissue was the most saturated, followed by subcutaneous then intramuscular tissue, for all bison treatments.
- There was no difference between treatments in the total saturated fatty acids content of intramuscular tissue.
- The polyunsaturated fatty acid content of Forage Fed and 50:50 Forage:Grain treatments was greater than the <90 Day Fed or Feedlot Finishing treatment, resulting in a more favorable PUFA to SFA ratio for the Forage Fed and 50:50 Forage:Grain treatments.

- The Forage Fed treatment had the greatest content of long chain omega-3 polyunsaturated fatty acids within the intramuscular tissue.
- Short term concentrate feeding, as with the <90 Day Fed treatment, was sufficient to reduce the content of the longer chained polyunsaturated fatty acids derived from α-linolenic acid.
- Although the 50:50 Forage:Grain treatment had access to forage, the concentrate available in the diet was sufficient to reduce the long chain PUFA content of the intramuscular tissue compared to the Forage Fed treatment, though not to the same extent as found in the <90 Day Fed treatment.
- Concentrate feeding, as with the Feedlot Finishing treatment, limited the amount in tissue of some of the most beneficial fatty acids to human health.
- The Forage Fed and 50:50 Forage:Grain treatments had the greatest content of linoleic acid within intramuscular tissue; this treatment pattern was not reflected in the *trans*vaccenic acid content of the tissue, where there was no treatment effect in intramuscular tissue.
- The majority of CLA *c*-9, *t*-11 found within bison tissue was located in the subcutaneous tissue for all treatments except the Feedlot Finishing treatment, which showed no tissue differences.
- Within intramuscular tissue, greater amounts of CLA *c*-9, *t*-11 were found in the Forage Fed and <90 Day Fed treatments, indicating short term concentrate feeding is insufficient to affect CLA *c*-9, *t*-11 content.
- The 50:50 Forage:Grain and Feedlot Finishing treatments, had the lowest CLA *c*-9, *t*-11 content within intramuscular tissue, indicating long term concentrate feeding affects CLA *c*-9, *t*-11 tissue content.
- Similar ($P>0.05$) proportions of linoleic acid were found in the Forage Fed and 50:50 Forage:Grain treatments while the Forage Fed and <90 Day Fed treatment were also similar ($P>0.05$; the Feedlot Finishing had the lowest amounts.
- Intramuscular omega-6 fatty acid content reflected the linoleic and arachidonic acid content, showing the 50:50 Forage:Grain and Forage Fed treatments to be similar, while the <90 Day Fed and Feedlot Finishing treatments were similar, with the former pair being greater than the latter.

More research is warranted into studying the effects of different concentrates and different feeding regimes on the fatty acid profile of bison. Results obtained during this study would suggest the overall effect of diet on tissue fatty acid composition would favor the Forage Fed treatment when viewed from a human health perspective. Forage Fed bison maximized the content of beneficial fatty acids within intramuscular tissue, compared to the Feedlot Finishing treatment. To maximize the desirable fatty acid composition of the lipid portion of bison meat, producers would benefit from maximizing the forage available to the bison throughout the finishing period.

4.0. Comparison of Fatty Acid Profiles of Bison, Beef and Sheep Finished Under Intensive Feeding Programs

4.1. Introduction

Finishing domestic animals for market on a high concentrate diet in a dry-lot setting is a common practice in North America. Most market cattle are placed in feedlots shortly after weaning. Motivation for feedlot finishing is to provide a more consistent product at a younger age under more economically structured conditions. High concentrate diets lend to a faster growing animal with a more uniform finish, as opposed to forage finishing were environmental factors may impede growth. Consumer perception of forage finished animals is that the meat has an "off-flavour" and yellow tinge to the fat caused by increased α-linolenic acid and carotenoid content (Griebenow et al. 1997). When finished to similar target end points, forage finished animals tend to be older (Mendell et al. 1998b), accumulating more of a "grassy" flavor to the meat (Wood et al. 2003). This is associated with an accumulation of α-linolenic and other highly unsaturated fatty acids that are more susceptible to oxidation within the meat. Ruminant adipose tissue generally is very saturated, making it firm. However, on high grain diets oleic acid begins to accumulate, resulting in a softer fat that may affect eating quality (Wood et al. 2003). Species differences have been noted when comparing fatty acid profiles of animals finished under feedlot conditions (Rule et al. 2002). Although diet is the most influential factor on fatty acid composition, sex differences (ie. castrated vs. non-castrated males) are also known to be factors (Rule et al. 1994).

Fatty acid comparisons between species under similar feeding operations help to illustrate the differences between specialty and traditional domestic livestock. Very little information is available comparing fatty acid profiles of bison to other domestic animals. Rule et al. (2002) compared bison and beef under both feedlot and forage finished conditions and found total fat to be affected more by diet than by species. Collecting fatty acid profiles from animals finished under commercial conditions will provide a greater understanding of the impact feeding management has on adipose tissues. How different species react to these diets can have an effect on management decisions regarding animals under intensive feeding programs.

The objective of this study was to compare species effects on the fatty acid profile of bison bulls, beef steers and sheep wethers finished to commercial standards under intensive feeding programs.

4.2. Materials and Methods

Animals used in this study included feedlot finished steers (n=4) and wethers (n=3). These animals were selected from one producer for each species and were fed typical barley-based finishing diets as found in western Canada. The animals were selected for slaughter according to typical visual assessment of finish commonly found in commercial practices. These animals were representative of feedlot finishing practices common to each species. Samples collected from steers and wethers were compared to previously collected tissues from Feedlot Finished bison (n=12). Tissue samples gathered from steers and wethers were collected and prepared in the same fashion as previously used to collect bison tissue samples (see section 3.2. of Materials and Methods). Samples included adipose tissue from the subcutaneous and perirenal areas as well as ribeye muscle (*longissimus dorsi*). Analyses of feedlot steer and wether tissues were conducted in the same manner as previously described in the bison finishing section (see section 3.2. of Materials and Methods).

4.3. Results

Lipid yields from freeze dried ribeye tissue extraction for intramuscular tissue from animals finished under feedlot conditions were as follows:
bison (0.0709 g g^{-1} tissue DM), beef (0.1539 g g^{-1} tissue DM),
sheep (0.2525 g g^{-1} tissue DM).

4.3.1. Fatty Acids C14 to C17 Chain Length

14:0 Myristic

Separation of effect ($P<0.05$) of tissue type indicated that while subcutaneous and perirenal tissues were similar ($P>0.05$), both contained more ($P<0.05$) myristic acid than did intramuscular tissue (Table 4.1.). Effect ($P<0.05$) of species showed a larger ($P<0.05$) proportion of myristic acid in beef than found in either bison or sheep tissue (Table 4.1.).

16:0 Palmitic

An interaction effect ($P<0.05$) between species and tissues was apparent for the palmitic acid content (Table 4.2.). Simple effects ($P<0.05$) showed that within perirenal tissue, beef had a greater ($P<0.05$) content of palmitic acid than either bison or sheep (Fig 4.1.), which were similar ($P>0.05$). Separation of simple effects ($P<0.05$) between species in intramuscular tissue showed beef and sheep to be similar ($P>0.05$) and to contain more ($P<0.05$) palmitic acid than bison (Fig 4.1.). Separation of simple effects ($P<0.05$) for tissue differences within species was evident for both bison and beef (Table 4.2.). Within bison, there was more ($P<0.05$) palmitic acid in subcutaneous and perirenal tissue than in intramuscular tissue (Fig. 4.2.). Tissue differences found in beef showed a larger ($P<0.05$) amount of palmitic acid in perirenal and intramuscular tissue than in subcutaneous tissue (Fig. 4.2.).

Minor C14 to C17 Fatty Acids

Minor fatty acids identified of carbon length 14 to 17 included myristoleic, pentadecanoic, palmitoleic, margaric and heptadecenoic acid.

There was an interaction effect ($P<0.05$) between tissues and species for myristoleic acid (Table 4.2.). A similar pattern in separation of simple effects ($P<0.05$) between species was observed across all tissues, with the content of myristoleic acid being greatest ($P<0.05$) in beef, with bison and sheep being similar ($P>0.05$). Tissue differences within species were apparent for bison and beef. In bison, intramuscular tissue was higher ($P<0.05$) in myristoleic acid than was subcutaneous or perirenal tissue. Beef accumulated a larger proportion of myristoleic acid in the subcutaneous tissue,

Table 4.1. Main effects for the fatty acid profile of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison, beef, and sheep fed under feedlot finishing conditions

		Species[z]				Tissue[z]				
		Bison	Beef	Sheep	P SEM	Subcutaneous	Perirenal	Intramuscular	P SEM	Effect
Fatty Acid		mg g-1 total fatty acid methyl esters								
14:0	Myristic	27.95 e	52.38 d	32.79 e	1.83	43.42 d	40.53 d	29.16 e	2.17	*ab*
14:1 *c*-9	Myristoleic	2.08	8.20	1.39	0.27	5.78	1.71	4.18	0.33	*c*
15:0	Pentadecanoic	12.37	8.28	5.73	1.25	5.94	5.07	15.37	1.48	*c*
16:0	Palmitic	222.32	273.11	254.51	7.85	239.58	264.21	246.16	9.32	*c*
16:1 *c*-9	Palmitoleic	25.89	41.58	25.85	1.99	38.31	25.16	29.85	2.37	*c*
17:0	Margaric	19.58 d	15.93 e	15.34 e	1.22	15.91	18.73	16.22	1.45	*a*
17:1 *c*-9	Heptadecenoic	3.58	6.02	3.75	0.26	4.69	2.66	5.99	0.31	*c*
18:0	Stearic	227.86 d	125.93 e	197.95 d	12.20	180.48 e	249.91 d	121.35 f	14.47	*ab*
18:1 *t*-9	Elaidic	1.66 d	0.63 e	0.85 e	0.27	0.54 e	0.65 e	1.95 d	0.32	*ab*
18:1 *t*-11	*Trans* vaccenic	21.65 e	47.71 d	12.12 f	2.48	31.46 d	31.62 d	18.40 e	2.94	*ab*
18:1 *c*-9	Oleic	355.08	365.02	400.45	12.11	392.55 d	320.61 e	407.39 d	14.37	*b*
18:1 *c*-11	Vaccenic	9.16	7.27	2.26	0.65	3.14	2.46	13.09	0.77	*c*
18:2 *c*-9,12	Linoleic	40.25	28.89	28.04	3.33	21.87	21.64	53.66	3.96	*c*
20:0	Arachidic	2.92	0.86	1.41	0.22	1.82	2.63	0.74	0.26	*c*
18:3 *c*-6,9,12	γ-Linolenic	0.20	0.19	0.83	0.14	0.14	0.11	0.98	0.16	*c*
20:1 *c*-11	Eicosenoic	0.27	0.37	0.20	0.05	0.20	0.23	0.41	0.06	*c*
18:3 *c*-9,12,15	α-Linolenic	9.92 d	5.20 e	5.70 e	0.89	6.80	6.44	7.59	1.05	*a*
18:2 *c*-9,*t*-11	CLA	3.49 d	4.26 d	2.10 e	0.40	4.14	3.00	2.70	0.48	*a*
18:2 *t*-10,*c*-12	CLA	0.02	0.39	0.10	0.03	0.22	0.07	0.22	0.03	*c*
20:2 *c*-11,14	Eicosadienoic	0.38	0.41	0.26	0.04	0.25 e	0.21 e	0.59 d	0.05	*b*
22:0	Behenic	0.15	0.17	0.14	0.03	0.06	0.14	0.27	0.03	*c*
20:3 *c*-8,11,14	Homo-γ-linolenic	1.06	1.26	0.50	0.11	0.48	0.45	1.88	0.13	*c*
20:3 *c*-11,14,17	Eicosatrienoic	0.16 d	0.08 e	0.10 e	0.02	0.07 e	0.08 e	0.19 d	0.02	*ab*
22:1 *c*-13	Erucic	0.28	0.15	0.13	0.08	0.18	0.15	0.23	0.09	
20:4 *c*-5,8,11,14	Arachidonic	7.56	3.34	4.71	1.43	0.92 e	0.80 e	13.88 d	1.70	*b*
22:2 *c*-13,16	Docosadienoic	0.17	0.13	0.07	0.03	0.07 e	0.07 e	0.22 d	0.04	*b*
20:5 *c*-5,8,11,14,17	Eicosapentaenoic	0.71	0.28	0.30	0.08	0.06	0.04	1.19	0.10	*c*
22:4 *c*-7,10,13,16	Docosatetraenoic	0.56	0.48	0.45	0.10	0.19 e	0.12 e	1.19 d	0.12	*b*
22:5 *c*-7,10,13,16,19	Docasapentaenoic	2.03	1.20	1.54	0.25	0.61	0.46	3.70	0.30	*c*
22:6 *c*-4,7,10,13,16,19	Docosahexaenoic	0.57	0.17	0.38	0.10	0.11	0.06	0.95	0.11	*c*

a-b, means within main effect differ (P<0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (P<0.05), shown on Table 4.2.
d-f, means within a row are different (P<0.05) for each main effect.
[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=12; beef subcutaneous, perirenal, and intramuscular tissue, n=4; sheep subcutaneous, perirenal, and intramuscular tissue, n=3.

Table 4.2. Interaction effects (*P* <0.05) for the fatty acid profile of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison, beef, and sheep fed under feedlot finishing conditions

			Bison n=12			Beef n=4			Sheep n=3			
			Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
Fatty Acid						mg g-1 total fatty acid methyl esters						
14:1	*c* -9	Myristoleic	1.62	0.88	3.73	14.75	3.37	6.47	0.97	0.87	2.34	0.56
15:0		Pentadecanoic	6.16	5.65	25.28	6.60	5.01	13.22	5.05	4.55	7.60	2.57
16:0		Palmitic	236.05	231.17	199.74	228.08	305.19	286.07	254.62	256.26	252.67	16.14
16:1	*c* -9	Palmitoleic	30.36	23.00	24.30	54.57	25.26	44.90	30.00	27.22	20.33	4.10
17:1	*c* -9	Heptadecenoic	2.82	2.09	5.82	7.23	2.47	8.37	4.02	3.42	3.79	0.53
18:1	*c* -11	Vaccenic	4.01	3.79	19.69	2.76	1.56	17.47	2.63	2.04	2.12	1.33
18:2	*c* -9,12	Linoleic	22.64	23.03	75.07	19.76	19.16	47.75	23.21	22.72	38.18	6.85
20:0		Arachidic	3.31	4.36	1.08	0.59	1.43	0.56	1.57	2.09	0.57	0.45
18:3	*c* -6,9,12	γ-Linolenic	0.07	0.05	0.49	0.10	0.09	0.38	0.24	0.19	2.07	0.28
20:1	*c* -11	Eicosenoic	0.11	0.10	0.61	0.33	0.36	0.42	0.16	0.24	0.19	0.11
18:2	*t* -10,*c* -12	CLA	0.04	0.03	0.00	0.61	0.13	0.44	0.03	0.04	0.22	0.06
22:0		Behenic	0.00	0.00	0.46	0.09	0.20	0.22	0.08	0.22	0.14	0.05
20:3	*c* -8,11,14	Homo-γ-linolenic	0.51	0.76	1.91	0.59	0.40	2.78	0.35	0.20	0.96	0.23
20:5	*c* -5,8,11,14,17	Eicosapentaenoic	0.04	0.03	2.05	0.04	0.02	0.79	0.10	0.08	0.73	0.17
22:5	*c* -7,10,13,16,19	Docasapentaenoic	0.46	0.38	5.25	0.28	0.17	3.15	1.09	0.82	2.70	0.52
22:6	*c* -4,7,10,13,16,19	Docosahexaenoic	0.05	0.03	1.64	0.01	0.01	0.48	0.26	0.15	0.73	0.20

[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=12; beef subcutaneous, perirenal, and intramuscular tissue, n=4; sheep subcutaneous, perirenal, and intramuscular tissue, n=3.

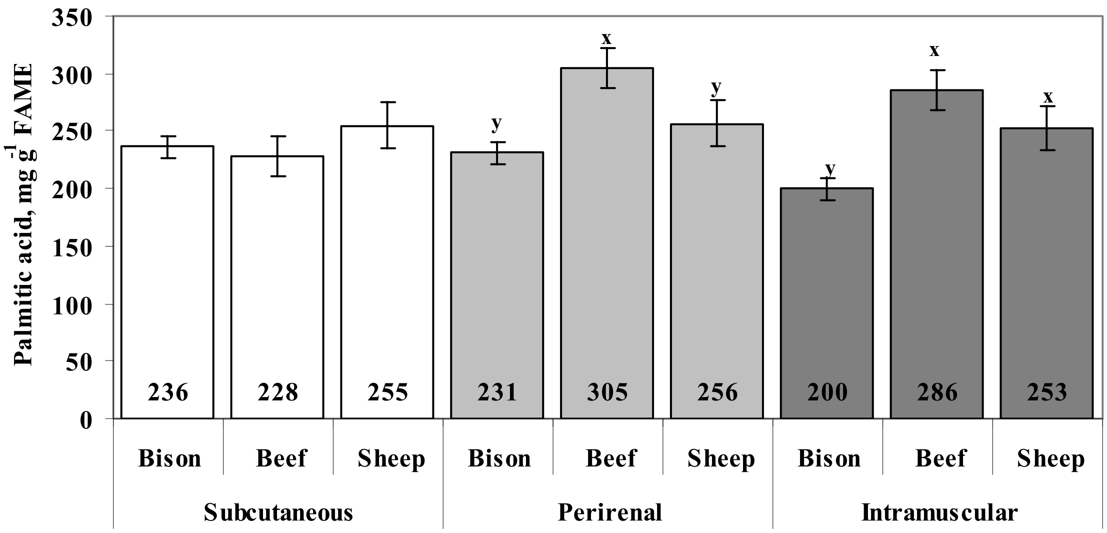

Figure 4.1. Species x tissue type interaction for palmitic acid (C16:0), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =9.88, beef=17.12, sheep = 19.77.

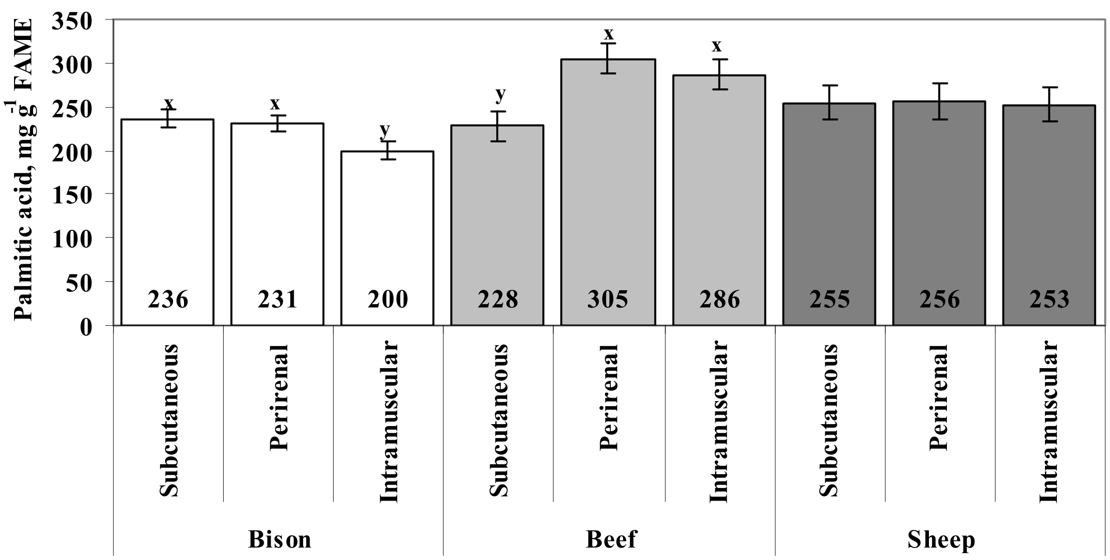

Figure 4.2. Species x tissue type interaction for palmitic acid (C16:0), means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =9.88, beef=17.12, sheep = 19.77.

followed by intramuscular tissue, with perirenal tissue having the lowest content. An interaction effect (*P*<0.05) for palmitoleic acid was observed between species and tissues (Table 4.2.). In both subcutaneous and intramuscular tissues, beef contained more (*P*<0.05) palmitoleic acid than bison or sheep. Between species, only beef showed tissue effects, with subcutaneous and intramuscular tissue having greater (*P*<0.05) amounts than perirenal tissue.

Of the odd chained fatty acids, separation of simple means for species differences within tissue types was observable in intramuscular tissue. In the intramuscular tissue, more (*P*<0.05) pentadecanoic acid was found in bison than in beef or sheep, which were similar (*P*>0.05). Only in bison were there tissue differences, shown by a larger (*P*<0.05) portion of pentadecanoic acid accumulating in intramuscular tissue than in the other tissues. Species effect (*P*<0.05) for margaric acid showed bison to have a greater (*P*<0.05) amount than found in either beef or sheep.

There was an interaction (*P*<0.05) between species and tissue types for heptadecenoic acid (Table 4.2.). Within subcutaneous tissue, beef had a greater (*P*<0.05) proportion than was found in bison or sheep. Within intramuscular tissue, beef had the highest (*P*<0.05) concentration of heptadecenoic acid, followed by bison, with sheep having the least (*P*<0.05) amount. Within bison, intramuscular tissue had the greatest (*P*<0.05) amount of heptadecenoic acid, with subcutaneous and perirenal tissue being similar (*P*>0.05). For beef, the heptadecenoic acid content of subcutaneous and intramuscular tissue was similar (*P*>0.05) and both tissues contained a greater (*P*<0.05) amount than was found in perirenal tissue.

4.3.2. Saturated and Monounsaturated Fatty Acids of C18 Chain Length

18:0 Stearic

Effect (*P*<0.05) of tissue for stearic acid content was the greatest (*P*<0.05) in perirenal tissue, followed by subcutaneous tissue, with intramuscular having the lowest (*P*<0.05) amount of stearic acid of the three tissues (Fig 4.3.). Effect (*P*<0.05) for

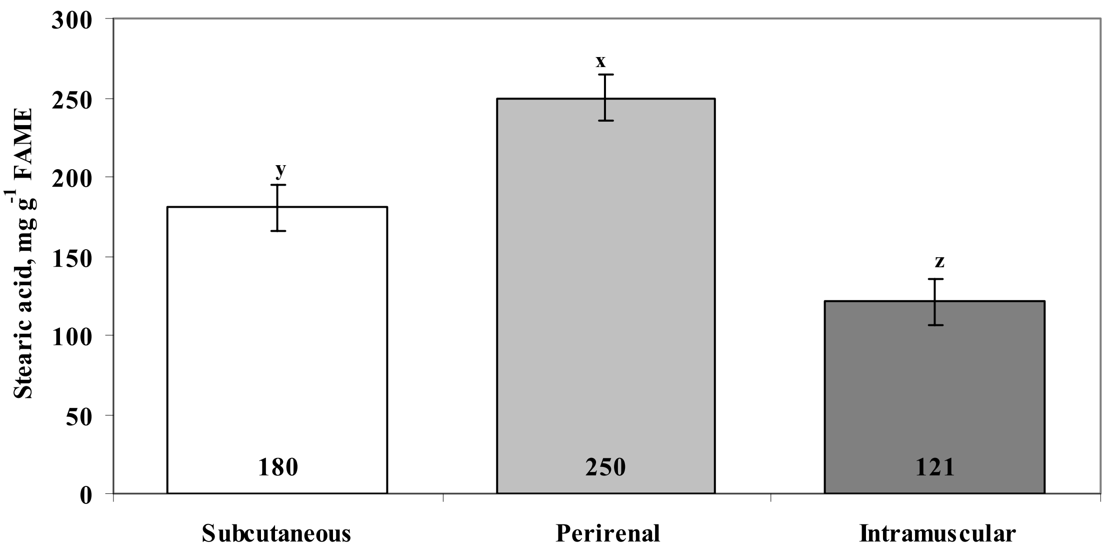

Figure 4.3. Effect of tissue type on stearic acid (C18:0) content under feedlot finishing conditions. Means followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for tissues =14.47.

species differences for stearic acid content indicate bison and sheep to be similar (P>0.05), both containing a greater (P<0.05) proportion than beef.

18:1 *t*-11 *Trans*vaccenic

Tissue effect (P<0.05) for *trans*vaccenic acid showed the content in subcutaneous and perirenal tissue to be indistinguishable (P>0.05), but both having more (P<0.05) than intramuscular tissue (Table 4.1.). Species separation effects (P<0.05) indicated beef to contain a larger (P<0.05) amount of *trans*vaccenic acid than either bison or sheep, which were similar (P>0.05).

18:1 *c*-9 Oleic

Separation of tissue type effect (P<0.05) showed that subcutaneous and intramuscular tissues contained relatively similar amounts of oleic acid (Table 4.1.), both containing greater (P<0.05) amounts than in perirenal tissue (Fig 4.4.).

Minor C18:1 Fatty Acids

Minor fatty acids identified in the C18 monounsaturated range included: elaidic and vaccenic acid. Effect (P<0.05) of species showed a larger (P<0.05) amount of elaidic acid present in bison than in beef or sheep, which were similar (P>0.05). Tissue effect (P<0.05) indicated that elaidic acid accumulated to a greater (P<0.05) degree in intramuscular tissue than in the other tissues.

An interaction (P<0.05) between tissue type and species were observed for vaccenic acid. Only within the intramuscular tissue were there species differences, which showed larger (P<0.05) proportions of vaccenic acid in bison and beef compared to sheep. Slice separation (P<0.05) for tissue differences within species were limited to bison and beef, both having greater (P<0.05) amounts of vaccenic acid located in the intramuscular tissue, compared to subcutaneous or perirenal tissue, which were similar (P>0.05).

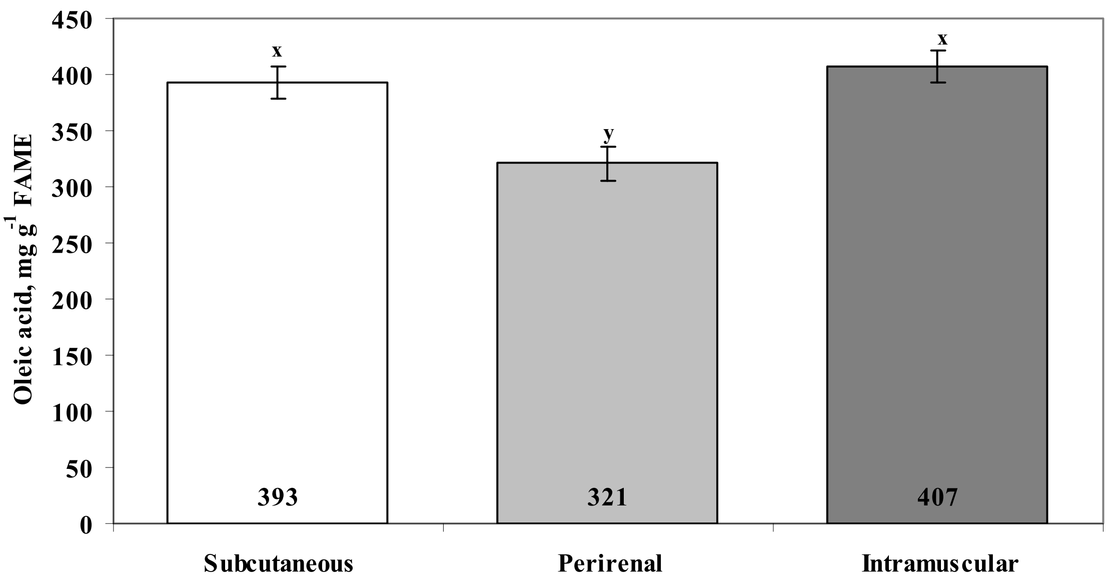

Figure 4.4. Effect of tissue type on oleic acid (C18:1 *c*-9) content under feedlot finishing conditions. Means followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for tissues =14.37.

4.3.3. C18 Diunsaturated, Conjugated Linoleic Acid and Polyunsaturated

18:2 *c*-9, 12 Linoleic

An interaction effect ($P<0.05$) between species and tissue types was observed for linoleic acid (Table 4.2.). Slice evaluation of species within tissues showed bison to containe more ($P<0.05$) linoleic acid than either beef or sheep in intramuscular tissue (Fig 4.5.). Separation of simple means for tissue within species showed that the intramuscular tissue had a larger ($P<0.05$) proportion of linoleic acid than either subcutaneous or perirenal tissue for both bison and beef groups (Fig 4.6.).

18:3 α-Linolenic

Effect ($P<0.05$) of species indicated bison contained greater ($P<0.05$) amounts of α-linolenic acid than did beef or sheep (Table 4.1.).

Conjugated Linoleic Acid Isomers

Effect ($P<0.05$) of species for the content of the conjugated linoleic isomer C18:2 *c*-9, *t*-11 was similar ($P>0.05$) in bison and beef, with both containing greater ($P<0.05$) amounts than sheep.

An interaction effect ($P<0.05$) was apparent between species and tissues for CLA c18:2 *t*-10, *c*-12 (Table 4.2.). Separation of simple effects ($P<0.05$) for species within subcutaneous tissue showed beef to have more ($P<0.05$) CLA *t*-10, *c*-12 than was found in bison or sheep (Fig. 4.7.). Within intramuscular tissue, separation of simple effects ($P<0.05$) showed beef having the most ($P<0.05$), followed by sheep, and with bison having the least ($P<0.05$) amount of CLA *t*-10, *c*-12 (Fig 4.7.). Slice separation of tissues within species showed that within beef, subcutaneous and intramuscular tissue contained similar ($P>0.05$) amounts of CLA *t*-10, *c*-12, both being greater ($P<0.05$) than the amount found in perirenal tissue (Fig 4.8.).

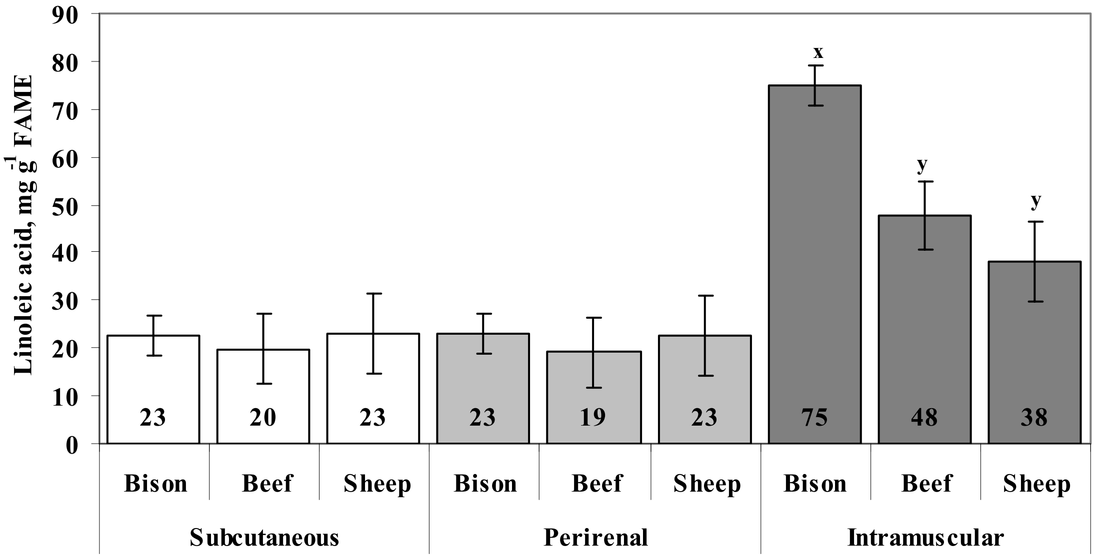

Figure 4.5. Species x tissue type interaction for linoleic acid (C18:2 *c*-9, 12), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =4.20, beef=7.27, sheep = 8.39.

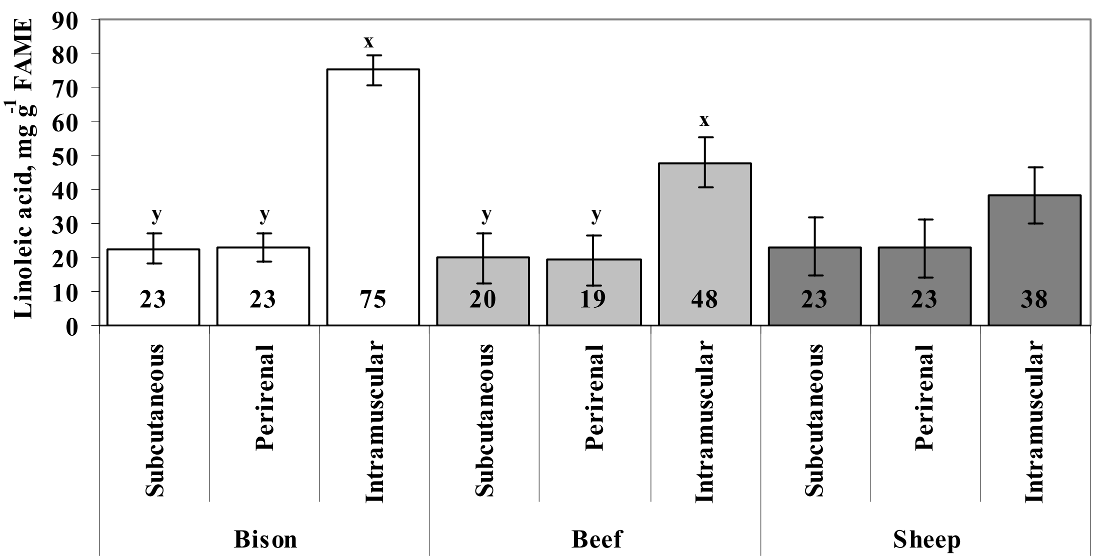

Figure 4.6. Species x tissue type interaction for linoleic acid (C18:2 *c*-9, 12), means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =4.20, beef=7.27, sheep = 8.39.

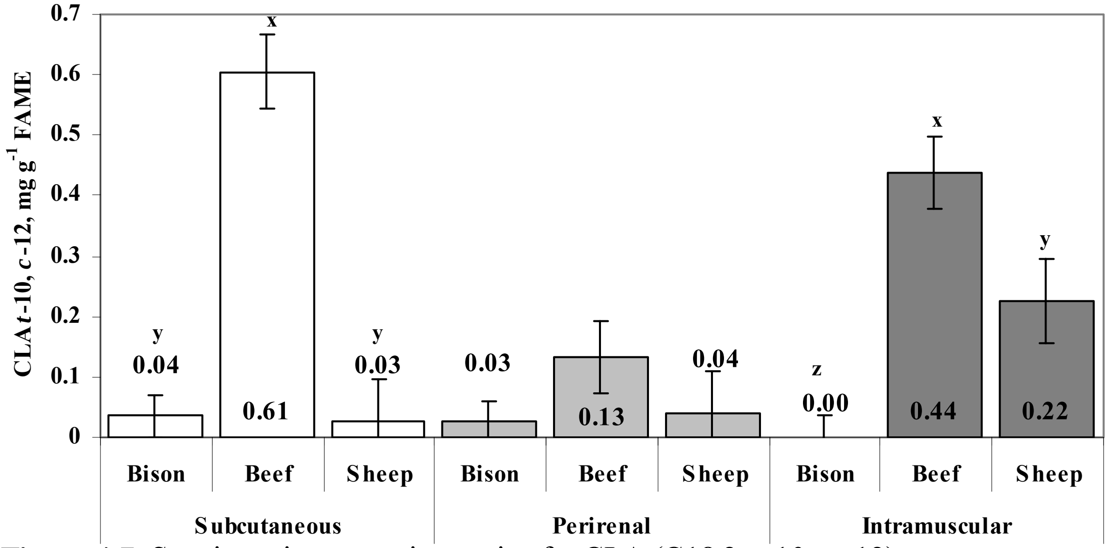

Figure 4.7. Species x tissue type interaction for CLA (C18:2 *t*-10, *c*-12), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.04, beef =0.06, sheep =0.07.

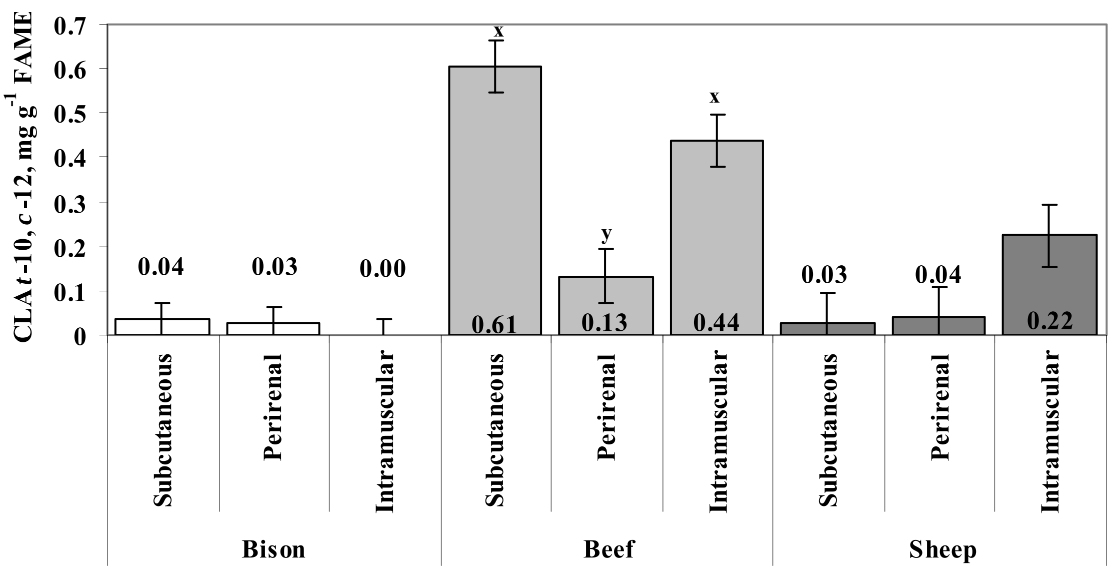

Figure 4.8. Species x tissue type interaction for CLA (C18 *t*-10, *c*-12), means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.04, beef =0.06, sheep =0.07.

Minor C18 Polyunsaturated Fatty Acids

The interaction (P<0.05) between species and tissue types show only minor amounts of γ-linolenic acid were detected (Table 4.2.). Simple effects (P<0.05) within intramuscular tissue indicated a greater (P<0.05) amount of γ-linolenic acid could be found in sheep as opposed to bison or beef (Fig. 4.9.). Separation of simple effects (P<0.05) of tissues within species indicated that within the sheep group, intramuscular tissue contained a larger (P<0.05) proportion of γ-linolenic than did subcutaneous or perirenal tissue.

4.3.4. Saturated and Unsaturated Fatty Acids of C20 to C22 Chain Length

20:4 Arachidonic

Effect (P<0.05) of tissue type for arachidonic acid indicates a greater (P<0.05) accumulation in the intramuscular tissue of all three species than was found in subcutaneous or perirenal tissue (Table 4.1.).

20:5 Eicosapentaenoic

Species within tissue interaction effects (P<0.05) were visible for eicosapentaenoic acid (Table 4.2.). Bison exhibited a larger (P<0.05) proportion of eicosapentaenoic acid in intramuscular tissue than did beef or sheep (Fig. 4.10.). Although only small amounts were detected, for both bison and beef, intramuscular tissue contained greater (P<0.05) amounts of eicosapentaenoic acid than either subcutaneous or perirenal tissue (Fig. 4.11.), which were similar (P>0.05).

22:5 Docosapentaenoic

There was an interaction effect (P<0.05) between species and tissue types for docosapentaenoic acid (Table 4.2.). Simple effect (P<0.05) separation for species within tissue show bison containing more (P<0.05) docosapentaenoic acid than beef or sheep in intramuscular tissue (Fig. 4.12.). In both bison and beef, intramuscular tissue contained a larger (P<0.05) proportion of docosapentaenoic acid than either subcutaneous or perirenal tissue (Fig. 4.13.).

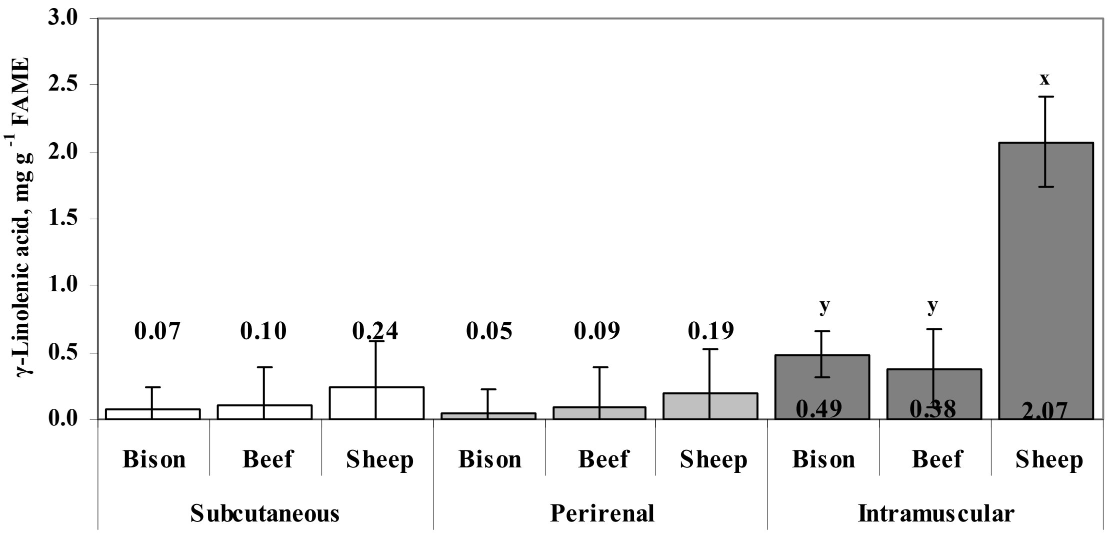

Figure 4.9. Species x tissue type interaction for γ-linolenic acid (C18:3 *c* -6, 9, 12), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.17, beef =0.30, sheep =0.34.

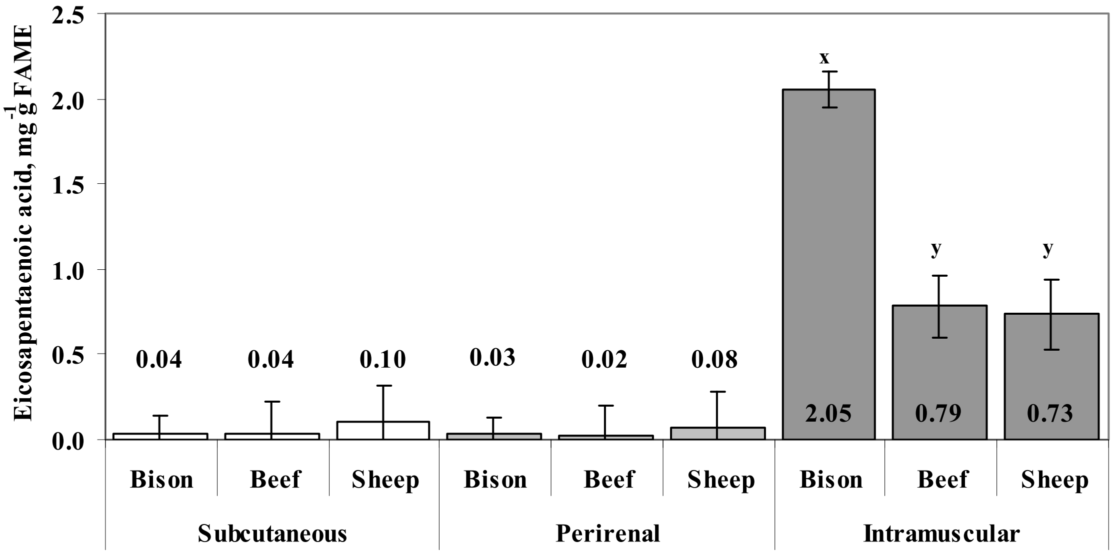

Figure 4.10. Species x tissue type interaction for eicosapentaenoic acid (C20:5), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for bison =0.15, beef =0.18, sheep =0.21.

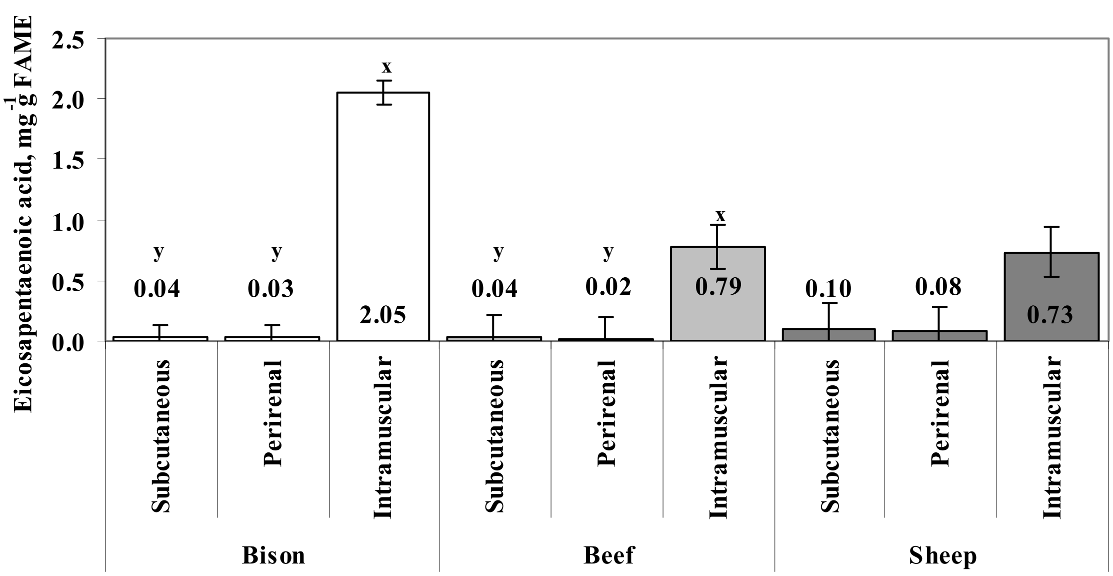

Figure 4.11. Species x tissue type interaction for eicosapentaenoic acid (C20:5), means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for bison =0.32, beef =0.55, sheep =0.64.

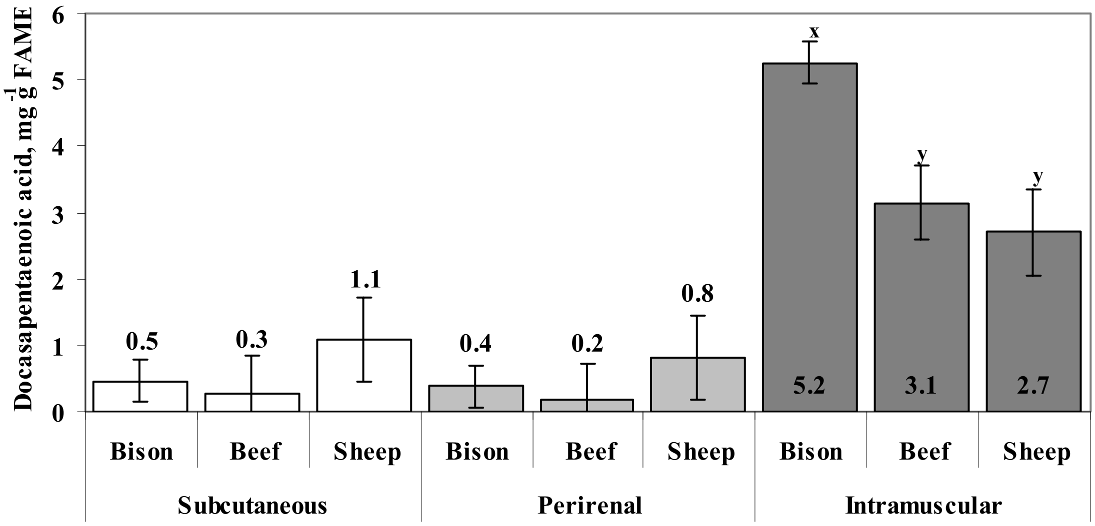

Figure 4.12. Species x tissue type interaction for docasapentaenoic acid (C22:5), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.32, beef=0.55, sheep =0.64.

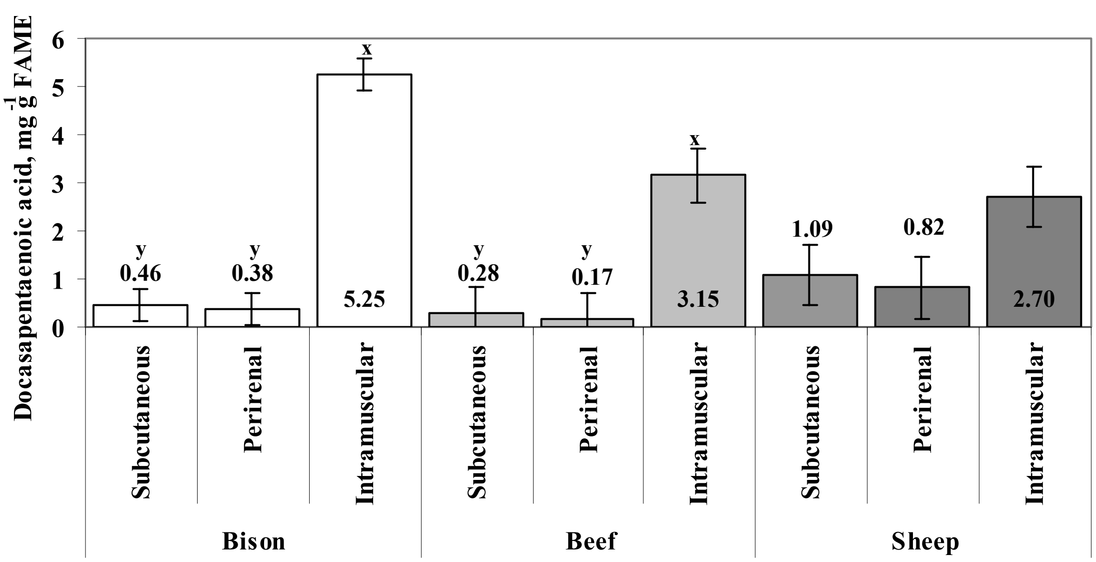

Figure 4.13. Species x tissue type interaction for docasapentaenoic acid (C22:5), means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.32, beef=0.55, sheep =0.64.

22:6 Docosahexaenoic

An interaction (*P*<0.05) between species and tissues was observable for the trace amounts of docosahexaenoic acid detected (Table 4.2.). Bison contained a larger (*P*<0.05) proportion of docosahexaenoic acid in the intramuscular tissue than was found in beef or sheep (Fig. 4.14.). Separation of simple effects (*P*<0.05) for tissues within species showed that within bison, intramuscular tissue had more (*P*<0.05) docosahexaenoic acid than did either subcutaneous or perirenal tissue.

Minor C20 to C22 Fatty Acids

Minor saturated fatty acids identified in the C20:0 to C22:0 range included arachidic and behenic acid. An interaction effect (*P*<0.05) amongst species and tissue types for arachidonic acid was identified (Table 4.2.). Bison contained greater (*P*<0.05) amounts of arachidic acid than beef or sheep, which were similar (*P*>0.05) in both the subcutaneous and perirenal tissues. Separation of simple effects (*P*<0.05) for bison, perirenal tissue contained more (*P*<0.05) arachidic acid than did subcutaneous tissue, with intramuscular tissue containing the least (*P*<0.05).

An interaction effect (*P*<0.05) for behenic acid was found between species and tissues (Table 4.2.). Simple effects (*P*<0.05) showed that both beef and sheep contained more (*P*<0.05) behenic acid than bison in perirenal tissue. Simple effects (*P*<0.05) for intramuscular tissue showed that bison contained more (*P*<0.05) than either beef or sheep. Separation of simple effects (*P*<0.05) for tissue type differences for behenic acid were only apparent in bison tissues, where intramuscular tissue contained more (*P*<0.05) than either subcutaneous or perirenal tissue.

Minor monounsaturated fatty acids identified in the C20:0 to C22:0 range included eicosenoic and erucic acid. There was an interaction (*P*<0.05) between species and tissue types for eicosenoic acid. Simple effects (*P*<0.05) showed bison having a greater (*P*<0.05) amount than was found in sheep, with beef being intermediate between the two (Fig. 4.15.). Tissue differences within species were only identified in bison, with intramuscular tissue having a greater (*P*<0.05) accumulation of eicosenoic acid than did subcutaneous or perirenal tissue. No differences between species or tissues were identified for erucic acid content.

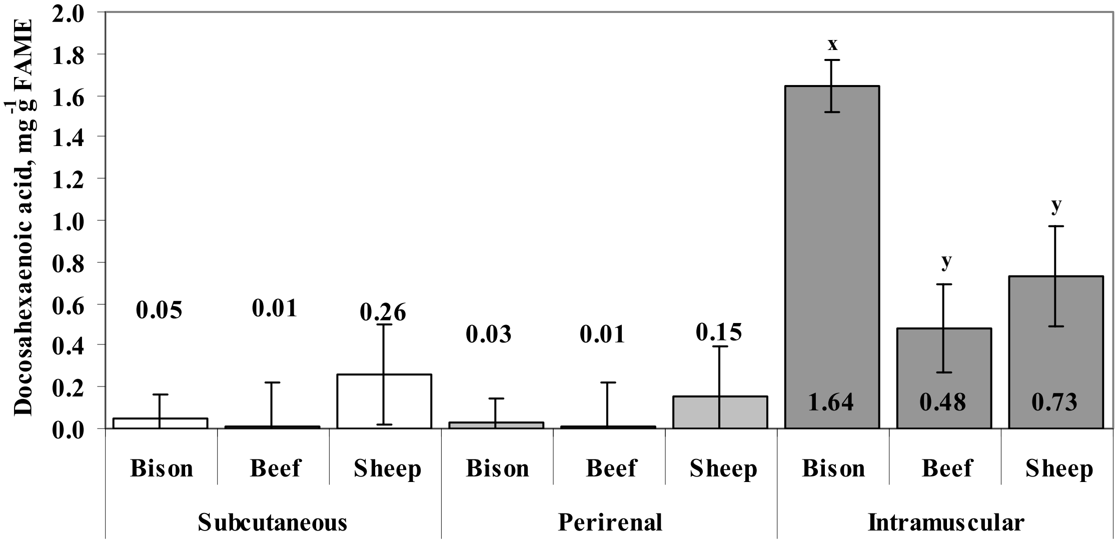

Figure 4.14. Species x tissue type interaction for docosahexaenoic acid (C22:6), means separation for species within tissue type under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.32, beef =0.55, sheep =0.64.

Minor polyunsaturated fatty acids identified in the C20:0 to C22:0 range included: eicosadienoic, homo-γ-linolenic, eicosatrienoic, docosadienoic and docosatetraenoic acid.

Effect (*P*<0.05) of tissue type was identified for eicosadienoic acid (Table 4.1.), with more (*P*<0.05) being found in intramuscular tissue than in subcutaneous or perirenal tissue.

Separation of simple effects (*P*<0.05) for species within tissues for homo-γ-linolenic acid indicated that for intramuscular tissue, beef contained the greatest (*P*<0.05) content followed by bison, with sheep having the lowest (*P*<0.05) levels detected (Table 4.2.). A greater (*P*<0.05) amount of homo-γ-linolenic acid was found in intramuscular tissue than in subcutaneous or perirenal tissue in both bison and beef.

Effect (*P*<0.05) of tissue for eicosatrienoic acid content (Table 4.1.) showed a greater (*P*<0.05) amount located in the intramuscular tissue than in subcutaneous or perirenal tissue. Effect (*P*<0.05) of species for eicosatrienoic acid indicated bison to have greater (*P*<0.05) accumulation than beef or sheep.

Effect (*P*<0.05) of tissue for docosadienoic and docosatetraenoic acid (Table 4.1.) showed a larger (*P*<0.05) amount in intramuscular tissue than in subcutaneous or perirenal tissue.

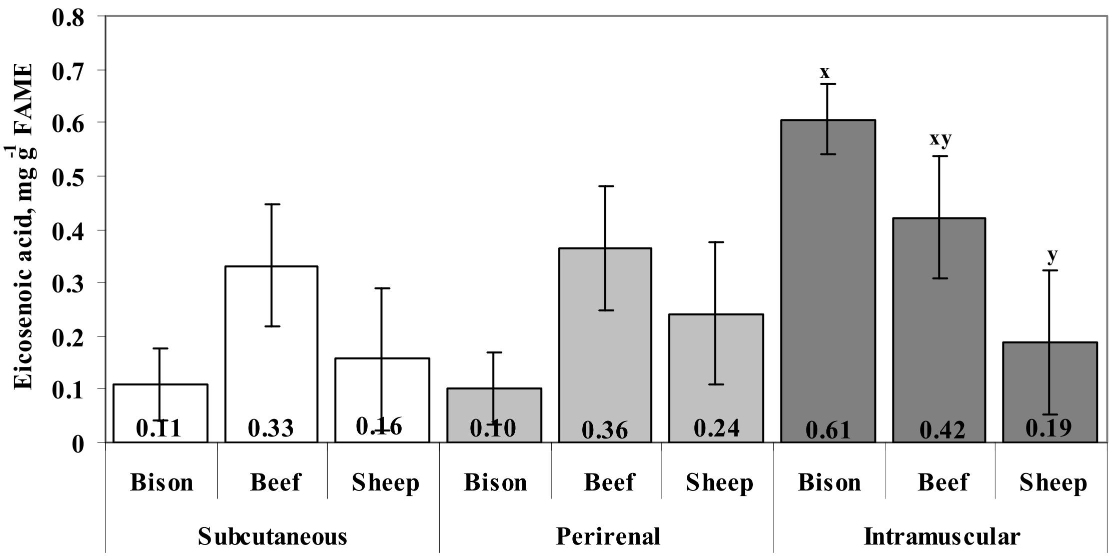

Figure 4.15. Species x tissue type interaction for eicosenoic acid (C20:1), means separation for species within tissue type under feedlot finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.07, beef =0.12, sheep =0.13.

4.3.5. Fatty Acid Totals and Selected Ratios

Interaction effects (*P*<0.05) between species and tissues for total saturated fatty acid (SFA) content are presented in Table 4.4.. In bison, the most (*P*<0.05) total SFA were located in perirenal tissue followed by subcutaneous, with intramuscular tissue having the least (*P*<0.05) (Fig. 4.16.). Within beef, perirenal tissue contained more (*P*<0.05) total SFA than either subcutaneous or intramuscular tissue, which were similar (*P*>0.05) (Fig. 4.16.). For sheep, perirenal and subcutaneous tissues were similar (*P*>0.05); both contained greater (*P*<0.05) amounts of total SFA than found in the intramuscular tissue (Fig. 4.16.). Differences between species for SFA content were apparent in subcutaneous tissue only, with similar (*P*>0.05) amounts being found in bison and sheep, both of which had a greater (*P*<0.05) amount than found in beef.

Interaction effects (*P*<0.05) between species and tissues types for the total amount of polyunsaturated fatty acids (PUFA) were observed (Table 4.4.). Within intramuscular tissue, bison contained more (*P*<0.05) PUFA than did beef or sheep (Fig. 4.17.), which were similar (*P*>0.05). Separation of simple effects for tissues within species showed that in both bison and beef, intramuscular tissue contained more (*P*<0.05) PUFA, while the subcutaneous and perirenal tissue were comparable (*P*>0.05).

There was an interaction effect (*P*<0.05) for the ratio of PUFA to SFA as shown in Table 4.4.. In intramuscular tissue, bison had a higher (*P*<0.05) ratio of PUFA to SFA than either beef or sheep, which were similar (*P*>0.05) (Fig. 4.18.). Simple effect (*P*<0.05) separation for tissues within species showed that in both bison and beef, the PUFA to SFA ratio was greater (*P*<0.05) in intramuscular tissue than in either subcutaneous or perirenal tissue.

Species effect (*P*<0.05) indicated that bison contained more (*P*<0.05) omega-3 fatty acids than did beef or sheep (Table 4.3.). Tissue effect (*P*<0.05) for the total amount of omega-3 fatty acids showed a higher (*P*<0.05) level in intramuscular tissue than either subcutaneous or perirenal tissue (Table 4.3.).

Table 4.3. Main effects for total fatty acid groups of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison, beef, and sheep fed under feedlot finishing conditions

	Species[z]				Tissue[z]				
	Bison	Beef	Sheep	P SEM	Subcutaneous	Perirenal	Intramuscular	P SEM	Effect
	mg g^{-1} total fatty acid methyl esters								
SFA	513.15	476.65	507.88	12.94	487.22	581.21	429.27	15.35	*c*
PUFA	67.06	46.28	45.08	5.45	35.93	33.54	88.96	6.46	*c*
PUFA/SFA[z]	0.15	0.10	0.10	0.01	0.08	0.06	0.21	0.02	*c*
ω-3[x]	13.38 d	6.93 e	8.03 e	1.01	7.64 e	7.08 e	13.63 d	1.19	*ab*
ω-6[y]	59.72	39.58	39.67	4.99	30.52	29.66	78.79	5.92	*c*
ω-6/ω-3	4.35 e	5.55 d	4.84 de	0.24	4.22 e	4.47 e	6.04 d	0.29	*ab*

a-b , means within main effect differ (*P* <0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (*P* <0.05), shown on Table 4.4.

d-f, means within a row are different (*P* <0.05) for each main effect.

[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=12; beef subcutaneous, perirenal, and intramuscular tissue, n=4; sheep subcutaneous, perirenal, and intramuscular tissue, n=3.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-3 fatty acids include 18:3 *cis* -9,12,15, 20:3 *cis* -11,14,17, 20:5 *cis* -5,8,11,14,17, 22:5 *cis* -7,10,13,16,19, 22:6 *cis* -4,7,10,13,16,19.

[w] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 *cis* -5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

Table 4.4. Interaction effects (*P* <0.05) of total fatty acid groups for subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison, beef, and sheep fed under feedlot finishing conditions

	Bison n=12			Beef n=4			Sheep n=3			
	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
	mg g^{-1} total fatty acid methyl esters									
SFA	537.84	594.07	407.90	402.82	574.72	452.78	520.99	574.84	427.94	26.59
PUFA	38.32	38.71	124.16	34.74	28.93	75.18	34.73	32.98	67.54	11.19
PUFA/SFA[z]	0.07	0.07	0.30	0.09	0.05	0.17	0.07	0.06	0.16	0.03
ω-6[y]	24.56	25.45	99.99	21.47	20.19	62.07	25.54	24.35	54.49	10.26

[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=12; beef subcutaneous, perirenal, and intramuscular tissue, n=4; sheep subcutaneous, perirenal, and intramuscular tissue, n=3.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-3 fatty acids include 18:3 *cis* -9,12,15, 20:3 *cis* -11,14,17, 20:5 *cis* -5,8,11,14,17, 22:5 *cis* -7,10,13,16,19, 22:6 *cis* -4,7,10,13,16,19.

[w] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 *cis* -5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

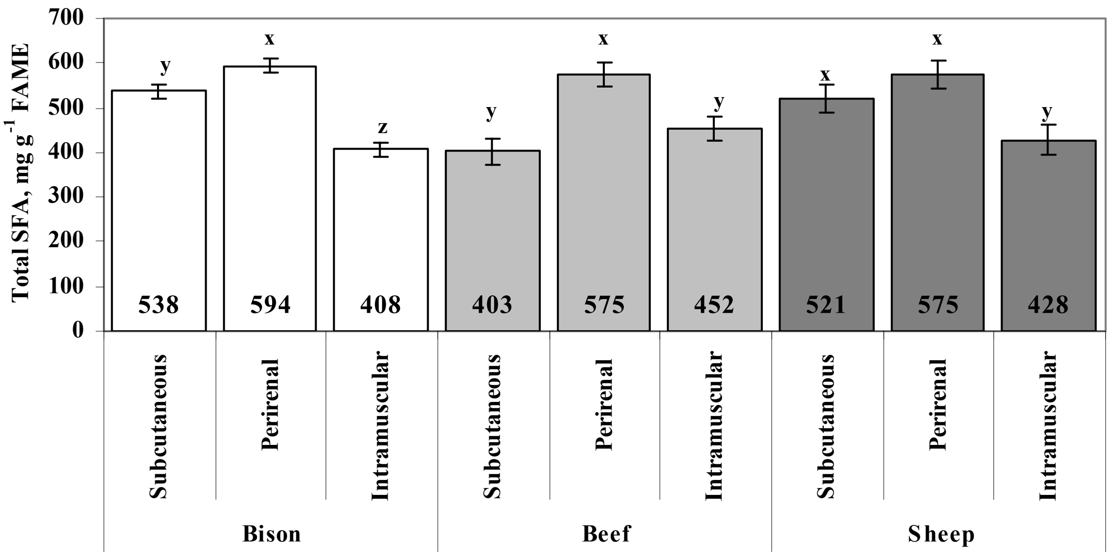

Figure 4.16. Species x tissue type interaction for total saturated fatty acids, means separation for tissue type within species under feedlot finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =16.28, beef =28.20, sheep =32.57.

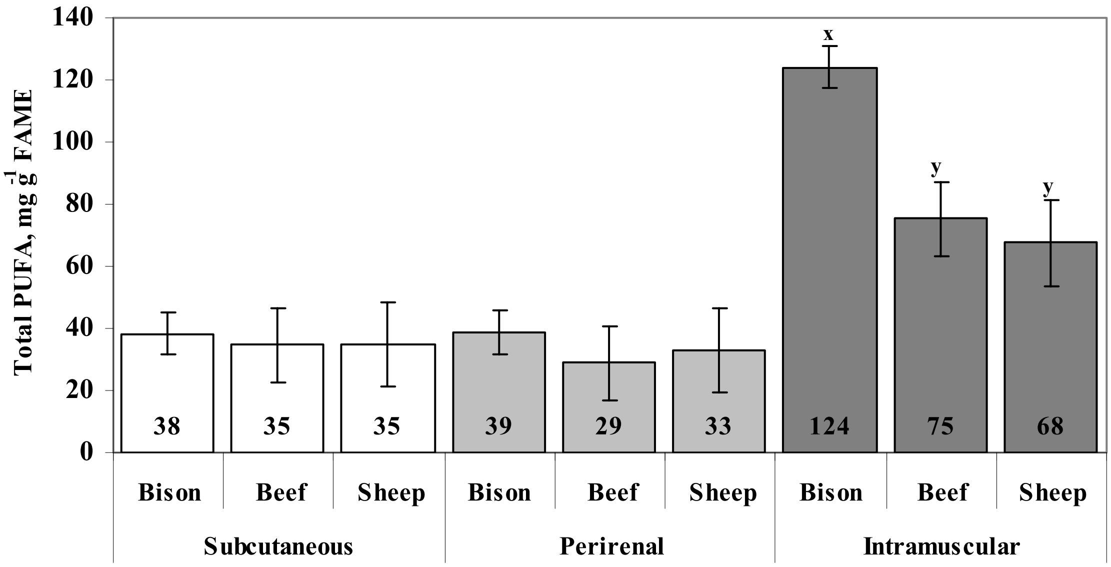

Figure 4.17. Species x tissue type interaction for total polyunsaturated fatty acids, means separation for species within tissue type under feedlot finishing conditions. Means within tissues followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =6.85, beef =11.87, sheep =13.71.

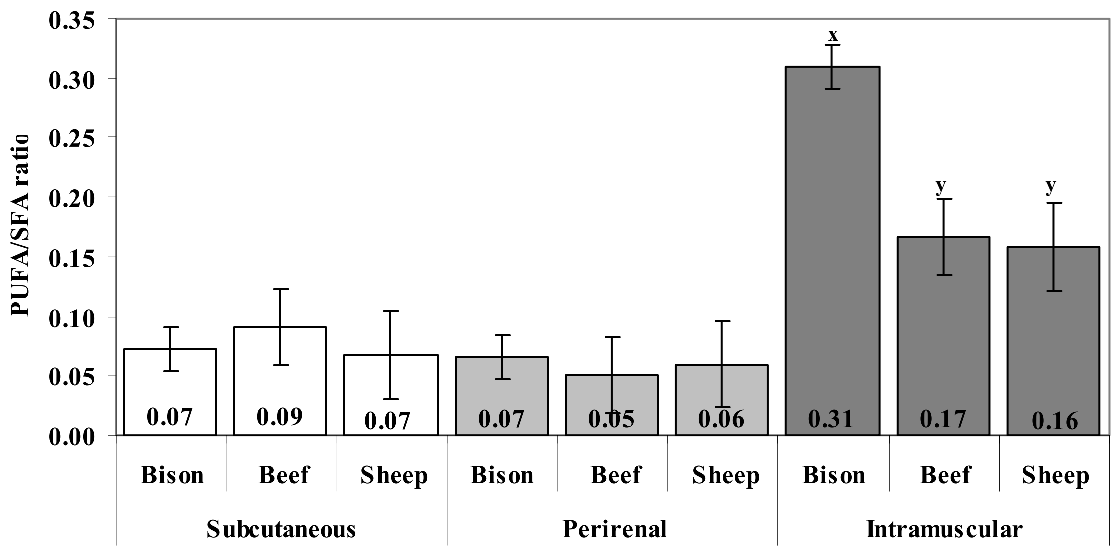

Figure 4.18. Species x tissue type interaction for the ratio of polyunsaturated to saturated fatty acids, means separation for species within tissue type under feedlot finishing conditions. Means within tissues followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.02, beef =0.03, sheep =0.04.

There was an interaction effect (*P*<0.05) between species and tissue types for the total omega-6 fatty acid content (Table 4.4.). The total amount of omega-6 fatty acids was greater (*P*<0.05) in bison than in beef or sheep within intramuscular tissue (Fig. 4.19.). Tissue differences within species were different only in bison and beef, where intramuscular tissue contained a greater (*P*<0.05) amount of omega-6 fatty acids than did subcutaneous or perirenal tissue.

The species effect (*P*<0.05) differences (Table 4.3.) indicated that beef had a higher (*P*<0.05) omega-6 to omega-3 ratio than was found in bison tissue, with sheep being intermediate (Fig. 4.20.). The tissue effect (*P*<0.05) for the ratio of omega-6 to omega-3 fatty acids was found to be greater (*P*<0.05) in intramuscular tissue than in subcutaneous or perirenal tissue (Table 4.3.).

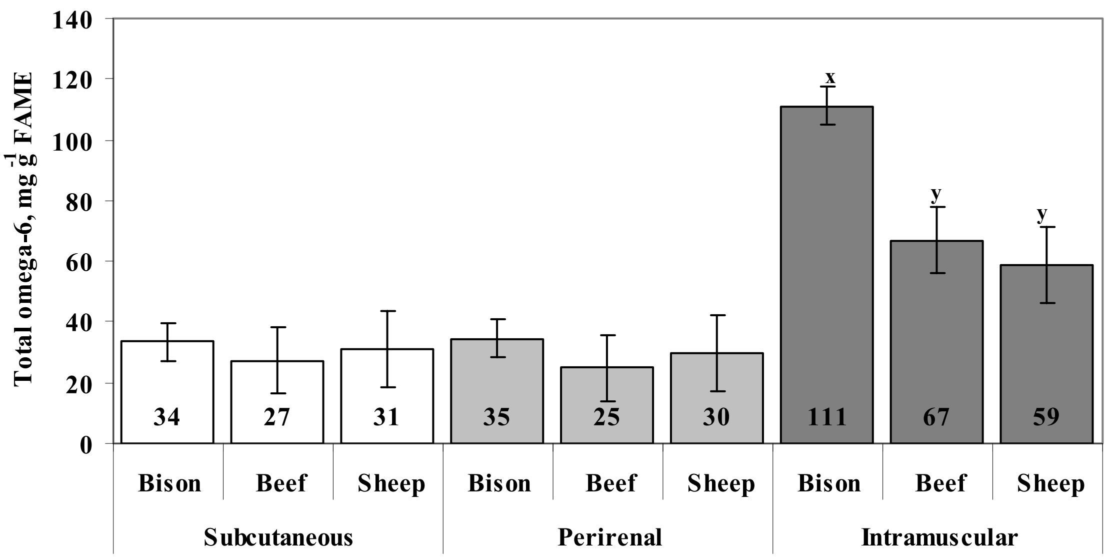

Figure 4.19. Species x tissue type interaction for total omega-6 fatty acids, means separation for species within tissue type under feedlot finishing conditions. Means within tissues followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.02, beef =0.03, sheep =0.04.

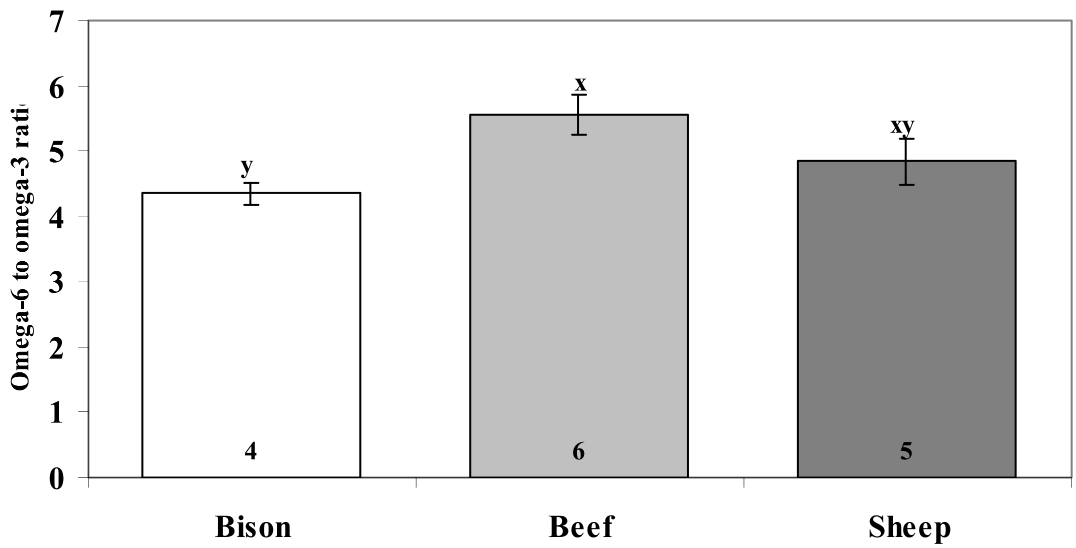

Figure 4.20. Effect of species on the ratio of omega-6 to omega-3 fatty acids of animals under feedlot finishing conditions. Means followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.18, beef =0.31, sheep =0.35.

4.4. Discussion

Commercial feedlot producers representing each of the three species supplied the tissue samples for this study. The samples collected from animals within this study are typical of those found under commercial conditions, and are representative of feedlot finishing practices currently used in western Canada for each species. Factors such as diet composition, time of slaughter, and age of animal at the time of slaughter were all decisions made by the individual producer, making feed intake and nutrient composition of the diet impossible to control or record. Information gathered during the study provides a one time look at the fatty acid profile of bison, beef, and sheep tissues produced under commercial feedlot finishing conditions.

Physiological factors such as the effect of castration and age of the animals were not accounted for and some leeway must be allowed when interpreting the comparisons. The fact that bison bulls were compared to lamb wethers and implanted beef steers will have an effect on the proportional deposition of fatty acids within adipose tissue. Koch et al. (1995) reported no significant difference between the amounts of intramuscular fat of the ribeye tissue when comparing bison steers to beef steers. Although visible marbling was observed in both beef and sheep ribeye muscle tissue in the present study, there was no observable marbling present within the bison ribeye muscle tissue. Comparison of beef bulls to steers by Rule et al. (1994) found bulls to have proportionally more linoleic and arachidonic acid in muscle tissue, while steers had higher oleic content when fed the same diet, indicating a greater proportion of phospholipids in bull tissue, most likely due to differences in degrees of marbling. As ruminants fatten, more monounsaturated fatty acids, particularly oleic acid, are deposited as intramuscular marbling (French et al. 2000). Changes to carcass fatness due to differences in energy intake may have a confounding effect on the fatty acid profile of the intramuscular fat. Tissues of ruminant animals tend to contain large amounts of saturated fatty acids as a consequence of the *de novo* synthesis of myristic and palmitic acids and extensive biohydrogenation of linoleic and α-linolenic acids in the rumen. The primary volatile fatty acid released by microbial activity within the rumen is acetate, which is the primary building block of fatty acid elongation within the tissue (St. John et al 1991). Increased amounts of highly digestible carbohydrates introduced into the rumen increases overall volatile fatty acid production and shifts the microbial population from a prominently fiber digesting (*Butyrivibrio fibrisolven*) to a primarily carbohydrate digesting population (amylolytic, lactobacillus) (Doreau and Ferlay 1994). As a result of this shift, proportionally more propionate is produced, absorbed and incorporated into the tissues (Loor et al. 2003). Concentrate diets have been shown to increase margaric content, while forage diets have increased pentadecanoic acid content (French et al. 2000). Increased deposition of *de novo* synthesized fatty acids in particular myristic and palmitic acid, are also linked to high concentrate diets (French et al. 2000), (Itoh et al. 1999), (Rule et al 2002).

The content of total saturated fatty acids was higher in the perirenal adipose tissue of all the species. These findings concur with those of Marmer et al. (1984) and Bolte et al. (2002), where a higher degree of saturation was found in the abdominal adipose tissue relative to that of subcutaneous tissue. Differences in total saturated fat content of intramuscular tissue between beef steers and bison bulls have indicated beef to contain significantly more saturated fat than bison (Rule et al. 2002). The fatty acid profile of intramuscular fat is similar to subcutaneous fat but generally contains more saturated fat in the form of stearic acid (Tume 2004).

The differences observed in the amount of total saturated fatty acids among the three species for subcutaneous tissue was due to the relative small amount of stearic acid present in the beef tissue. Minor differences between the amounts of saturated fatty acids exists for all saturated fatty acids, except for stearic acid, where beef contains half as much compared to bison or sheep subcutaneous tissue. As more fatty acids are synthesized, there is increased elongation and desaturation activity (St. John et al. 1991). Fatty acid elongation activity has been found to be higher than the desaturase activity within subcutaneous adipose tissue (St. John et al. 1991).

Although the total amount of saturated fatty acids is not different among species for intramuscular tissue, the relative proportion of certain fatty acids present within the tissue is of a concern from a human health perspective. The average myristic acid content of beef tissues was 47% and 37% greater than that found in either bison or sheep tissues respectfully. Palmitic acid content was greater by 30% and 21% in beef and sheep, respectively, than in bison intramuscular tissue. High concentrate rations generally promote the formation of *de novo* synthesized fatty acids (Loor et al. 2003), which tend to accumulate in intramuscular fat deposits as the animal approaches maturity. Stearic acid content was shown to vary by tissue, with perirenal tissue having the greatest content and subcutaneous and intramuscular tissue being only 72% and 48% that of perirenal tissue. No species effect was observed in this trial. Changes to tissue stearic acid content are mixed, with levels decreasing or not being affected by concentrates (Mandell et al. 1998b). Similar to the findings of Rule et al. (2002), within intramuscular tissue, greater amounts of margaric acid than pentadecanoic acid were found in feedlot beef. However, in feedlot bison, greater amount of pentadecanoic acid than margaric acid were found in intramuscular tissue. The risk from excess saturated fatty acids in the diet is the resulting effect on plasma cholesterol levels, in particular the level of low-density lipoproteins in the plasma, although stearic acid has not been shown to have any effect on cholesterol levels (Rhee 2000).

Polyunsaturated fatty acids are generally 18-carbons or longer and contain two or more double bonds. Polyunsaturated fatty acids are most often associated with phospholipids due to the specificity of the acyl-transferase. Very little PUFA are encountered in subcutaneous or perirenal tissues, as the majority of these lipid storage sites are comprised of triacylglycerides surrounded by a thin membrane layer (Hunt and Groff 1990). However, muscle tissue contains considerable portions of PUFA's in their membrane layers which contribute to cell fluidity (Lees 1990). As expected, there were only small, indistinguishable amounts of PUFA found in the subcutaneous and perirenal tissue for all species. The proportion of polyunsaturated fatty acids located in muscle tissue depends on the degree of intramuscular infiltration of adipose deposits. Within species, both bison and beef intramuscular tissues contained more polyunsaturated fatty acids than found in their respective subcutaneous or perirenal tissue. The observation that there was no difference between sheep tissues for total polyunsaturated fatty acid content could be illustrative of the degree of marbling within the intramuscular tissue. Bison had a higher proportion of polyunsaturated fatty acids than beef or sheep, which had only 60% and 55% of the total polyunsaturated fatty acid content of bison intramuscular tissue. The clear separation between species may be due to the limited, if existent, amount of marbling present within bison muscle tissue. Such differences observed between species could be exaggerated due to the physiological age of the animal and the degree of finish at the time of slaughter.

Indications from the ratio of polyunsaturated to saturated fatty acids showed bison to have twice as high a ratio as that found for beef and sheep. Given the equivalent amount of total saturated fatty acids found in the intramuscular tissue for all three species, the difference would be dependent on the relative amount of polyunsaturated fatty acids found within the tissue. Bison clearly contain a higher proportion of polyunsaturated fatty acids within the intramuscular tissue, thus the higher ratio than was found in beef or sheep.

The absence of observable marbling within the bison ribeye tissue would be sufficient to account for the differences shown when comparing intramuscular fatty acid profiles of bison to those of beef or sheep. Similar dilutions of polyunsaturated fatty acids were noted in steers by Rule et al. (1995) when compared to beef bulls. Energy content of the diet is the most significant factor affecting an animal's ability to form intramuscular fat deposits, as shown in numerous studies with beef or sheep. Growth hormone levels, such as testosterone from non-castrated male animals, may have an effect on the time an animal takes to reach physiological maturity and may have an effect on the overall level of finish/marbling an animal achieves. Koch et al. (1995) reported that although bison steers did show visible amounts of marbling, it was not as substantial as that of beef steers. Bison bulls are presumably still growing and laying down more lean tissue at the time of slaughter than are the steers or wethers. Hormone levels could have had an influence on the results by affecting the physiological stage of growth of the animal at the time of slaughter. Rule et al. (1994) found bulls to have lower lipid content than steers fed equivalent diets at the same age. If all animals were finished to the same level of backfat, relative differences between species most likely would be affected.

Greater amounts of linoleic acid found in intramuscular tissue of bison compared to beef or sheep would suggest greater bypass of PUFA's through decreased lipolysis or decreased rates of biohydrogenation. Oilseeds contain greater amounts of lipid than cereals and generally are high in oleic and linoleic acid with lesser amounts of palmitic and α-linolenic (White 2000). Differences observed between tissue fatty acid profiles of the different species most likely relate to the substrates available from the diet. Linoleic and oleic acid are the primary fatty acids found in cereal grains (Becker 2000), with lesser amounts of stearic and palmitic acid also present. Inclusion of extruded oilseeds within a ruminant diet would act as an energy-rich protein source. The ratio between linoleic and *trans*vaccenic acid within the intramuscular tissue would suggest a more rapid rate of biohydrogenation from linoleic to *trans*vaccenic acid in beef followed by sheep with bison having the slowest saturation rate.

The *c*-9, *t*-11 isomer is the most abundant form of CLA found in ruminant products. The *c*-9, *t*-11 CLA precursor, *trans*vaccenic acid is an intermediate in the biohydrogenation of linoleic and linolenic acid. A higher content of *trans*vaccenic acid within the tissues would suggest a greater accumulation within the rumen and a subsequent absorption into the tissues. *Butyrivibrio fibisolvens* hydrogenates linoleic and the linolenic acids to *trans*vaccenic, but only two *Fusocillus* species have been identified that can convert *trans*vaccenic acid to stearic acid. When placed in a mixed culture, *B. fibisolvens* out competes the *Fusocillus* species, thus causing a build up of *trans*vaccenic acid (Harfoot and Hazlewood 1997). Since α-linolenic acid is usually only found in significant quantities in association with green forages, the *trans*vaccenic acid probably originated from linoleic acid. The most probable explanation for observed differences would be dietary differences, most notably linoleic acid content. Although no feed analysis was conducted, sources of linoleic acid within typical feedlot diets would be from the cereal grains (Wood et al. 2003) other likely sources can include oilseeds (Rule et al. 1994) or silage (Noci et al. 2005). Current finding from this study show the *c*-9, *t*-11 CLA content was notably higher in beef and bison than sheep indicative of a higher content of linoleic acid in the diet as well as a greater absorption of *trans*vaccenic acid.

Limited amounts of 10-*trans*-octadecenoic acid are also produced in the rumen, usually as a result of a shift in the bacterial fauna caused by increased concentrates in the diet. This population shift would favor the formation of *trans*-10-octadecenoic acid (Griinari and Bauman 1999). As with *trans*vaccenic acid, the conversion of *trans*-10 octadecenoic acid to stearic acid is the rate-limiting step due to the specificity of the two *Fusocillus* species (Harfoot and Hazlewood 1997). Subsequent absorption in the small intestine and incorporation into the tissues followed by further desaturation, gives rise to increased levels of CLA *t*-10, *c*-12 within the tissues. The higher content found in beef tissues may be a reflection of a shift to a lower rumen pH, coupled with a richer source of linoleic acid in the diet than was found in that of bison or sheep.

Linoleic acid acts as the primary precursor to the omega-6 family of fatty acids. The greater amounts of linoleic acid escaping the rumen will have a subsequent effect on the amount of omega-6 fatty acids, especially arachidonic acid accumulating in the tissues. Intramuscular tissue contains the largest proportion of linoleic acid due to its association with membrane phospholipids in the muscle tissue. Of the three species, bison had the largest deposit of linoleic acid within the intramuscular tissue, having 36% greater content than beef, and twice the content of sheep intramuscular tissue. Elongase and desaturase products of linoleic acid were all greater in bison tissue; however, the conversion from linoleic to arachidonic acid varied among species. The ratio was similar for bison and sheep (3.5:1), but beef was higher (5.1:1). This could imply more efficient conversion of linoleic to arachidonic in bison and sheep. Arachidonic acid acts as the precursor for the series-2 prostaglandins and series-4 leukotrienes (Calder and Grimble 2002). Eicosanoids derived from omega-6 fatty acids are widely acknowledged as having pro-inflammatory effects on the body's immune system. Total omega-6 tissue content for subcutaneous and perirenal tissue was similar for all three species. Total omega-6 content was greatest within bison intramuscular tissue being 40% and 47% higher than beef or sheep intramuscular tissue respectively, possibly reflecting a diet richer in linoleic acid and a greater passage of linoleic acid from the rumen. Possible species differences would include a greater proportion of PUFA in bison intramuscular tissue due to diffuse marbling within the intramuscular tissues. Greater passage of linoleic acid through the rumen and subsequent changes within the tissue all contribute to the increased content of omega-6 fatty acids within the intramuscular tissue. Possible lower lipolysis or biohydrogenation efficiency within the rumen due to decreased pH would increase the amount of bypass linoleic acid available for absorption and incorporation into tissues.

The amount of α-linolenic acid found within the tissue has a direct influence on the amount of individual elongase and desaturase derivatives of α-linolenic acid, as well as having the greatest effect on the total omega-3 content of the tissue. The long-chained omega-3 polyunsaturated fatty acids were mainly located in intramuscular tissue and were found in higher levels in bison, being 40% and 52% greater than in beef and sheep, respectively. The hypolipidemic effects attributed to omega-3 fatty acids are only applicable to the longer-chain desaturase and elongase products of α-linolenic acid, as α-linolenic acid does not appear to have an effect on triglyceride concentrations in the blood (Simopoulos 2000). Increased dietary intake of omega-3 polyunsaturated fatty acids reduces the incidence of coronary heart disease, which may be independent of any effects these fatty acids have on lipid levels in the blood (Simon et al. 1995).

Differences between the species within the intramuscular tissue indicated that bison had 2.6 and 2.8 times the eicosapentaenoic acid content of beef and sheep respectively. Eicosapentaenoic acid is the precursor for the anti-inflammatory eicosanoids of the series-3 prostaglandin and series-5 leukotriene family. There is a preference towards omega-3 fatty acids by the enzymes responsible for the elongation and desaturation of α-linolenic acid and linoleic acid (Chapkin 2000); however, there will always be a greater proportion of omega-6 fatty acids due to the abundance of linoleic acid found in feeds. Relative amounts of eicosanoids produced within the body are based on the proportion of omega-6 and omega-3 fatty acids within the tissue (Pediatrika 2004). During the formation of eicosanoids, eicosapentaenoic acid is preferentially incorporated into production rather than arachidonic acid (Chapkin 2000; Simpoulos 2002; Pediatrika 2004). The way in which the actions of eicosanoids are exhibited within the body is through negative inhibition. Omega-3 eicosanoids have a greater inhibitory action on omega-6 eicosanoids than omega-6's have on omega-3 eicosanoids, hence the omega-3's apparent anti-inflammatory properties (Pediatrika 2004).

The docosapentaenoic acid content within the intramuscular tissue of beef and sheep were, respectively, 60% and 53% to that of bison. Docosapentaenoic acid has been shown to be the most potent inhibitor of blood platelet aggregation compared to its precursor, eicosapentaenoic acid, or its successor, docosahexaenoic acid (Akiba et al. 2000). The relation of docosapentaenoic to docosahexaenoic acid was most similar between bison and sheep, with conversions of 3.2:1 and 3.70:1 respectively. Beef had a much higher ratio at 6.56:1, which could suggest a slower conversion from docosapentaenoic to docosahexaenoic acid. The docosahexaenoic acid content of the intramuscular tissue of bison was 3.4- and 2.2-fold greater than that of beef or sheep, respectively.

Species differences for the omega-6 to omega-3 fatty acid ratio were observed among bison, beef and sheep fed under feedlot conditions. The omega-6 to omega-3 fatty acid ratio ranged from 4.35 to 5.55, with bison being the lowest and beef the highest, with the sheep ratio being similar to both species. Similar findings by Rule et al (2002) showed an omega-6 to omega-3 ratio of 5.73 and 6.38 for feedlot bison and beef, respectively.

4.5. Summary and Conclusions

Comparisons of species differences as represented by the results presented within this study for feedlot finished animals, from a human health point of view bison appears to have a more favorable pattern compared to beef and sheep based on their respective fatty acid profiles. Preliminary results drawn from the comparison of commercially feedlot finished species within this study include:

- Total saturated fatty acid contents of intramuscular tissue are similar, but bison contained the lowest amounts of myristic acid and the hypercholesterolemic acid, palmitic acid.
- Total polyunsaturated fatty acid content of intramuscular tissue was greater in bison than in either beef or sheep.
- The PUFA to SFA ratio of bison intramuscular tissue was nearly twice of that of beef or sheep intramuscular tissue.
- The proportionally higher content of PUFA's within the intramuscular tissue of bison led to a greater content of both omega-6 and omega-3 fatty acids.
- The level of conjugated linoleic acid *c*-9, *t*-11 was similar ($P>0.05$) in both bison and beef intramuscular tissue, with sheep containing proportionally less ($P<0.05$).

- Although only minor amounts were detected, proportions of CLA *t*-10, *c*-12 in beef subcutaneous tissues were six-fold greater and two- to four-fold greater in intramuscular tissue than found in bison or sheep tissue, respectively.
- The ratio of omega-6 to omega-3 fatty acids was lowest for bison (4:1), and highest for beef (6:1), with sheep being intermediate (5:1).

From a human health perspective, the fatty acid profile found in bison bulls fed under feedlot finishing conditions would be superior to the fatty acid profile of either beef steers or sheep withers. Further research into the effects of diet on the fatty acid profile of bison is needed in order to fully explore species differences under different commercial feedlot finishing strategies. The observation that bison intramuscular tissue contained greater amounts of omega-3 fatty acids could be caused by a difference between species. However, current results could be confounded by the level of finish each animal achieved prior to slaughter. Further comparisons of species under more controlled conditions would be warranted.

5.0. Evaluation of the Effect of Species on the Fatty Acid Profile of Bison and Sheep Finished on Forage Diets

5.1. Introduction

Although finishing ruminant animals on forage is not common practice in North America, there is renewed interest given the potential benefits to meat fatty acid composition. Finishing animals on grasslands is not a new development, in fact only in North America is it a common practice to extensively finish animals on concentrate-based diets. Forage based finishing systems utilize much of the marginal grasslands throughout the world such as those found in Australia or Brazil. Forage finishing systems are also utilized with more productive grasslands such as those found in New Zealand. Prior to conservation efforts initiated in the late 1800's, bison thrived on the grasslands of North America. It is unlikely that today's farmed bison finished on forage would differ much from their wild ancestors. Analysis of forage finished bison offers a unique look at what was available to early pioneers compared to other forage fed domestic stock. Although not as popular in North America, sheep production makes a large contribution to global ruminant production. Some of the major sheep producing countries include Australia, China, Iran, and New Zealand, where grass finishing sheep is the traditional practice. In the interests of improving human health, a push is being made to return to a diet resembling that of a pre-industrialized society (Simopoulos 2000). Although forage finished animals tend to have a yellow tinge to the fat caused by the accumulation of fat-soluble pigments such as β-carotene, Knight and Death (1997) found no adverse health effects associated with it. Fresh forages have sufficient tocopherol content to enhance meat colour stability by suppressing the auto-oxidation of oxymyoglobin to metmyoglobin (Daly et al. 1999). Human health benefits attributed to prolonged forage finishing of ruminant animals are numerous (Marmer 1984, Rule et al. 2002, Marchello and Driskell 2001).

The objective of this study was to compare the fatty acid profile of bison finished on forage to that of Merino sheep finished on forage.

5.2. Materials and Methods

Merino sheep wethers (n=3) used for this study originated from one producer. Wethers were grazed on mixed seeded pasture and native prairie paddocks and were representative of common forage finishing practices. The animals were selected for slaughter according to typical visual assessment of finish commonly found in commercial practices. Samples collected from forage-finished sheep were compared to previously collected tissues from Forage Fed bison (n=19). Tissue samples gathered from forage finished sheep were collected and prepared in the same fashion previously used to collect bison tissue samples (see section 3.2. of Materials and Methods). Samples included adipose tissue collected from the subcutaneous and perirenal areas as well as intramuscular lipid collected from ribeye muscle (*longissimus dorsi*). Analysis of sheep tissues was conducted in the same way as previously described in the bison finishing section (see section 3.2. of Materials and Methods).

5.3. Results

Lipid yields from freeze dried ribeye tissue extraction of intramuscular tissue from animals finished on forage were as follows: bison (0.0529 g g^{-1} tissue DM), sheep (0.1316 g g^{-1} tissue DM).

5.3.1. Fatty Acid C14 to C17 Chain Length

14:0 Myristic

There was an interaction effect (P<0.05) between species and tissue types for myristic acid (Table 5.2.). Separation of simple effects (P<0.05) for species by tissue type shows sheep containing more (P<0.05) myristic acid than bison in all tissues (Fig 5.1.). Within bison, separation of simple effects (P<0.05) for myristic acid content found subcutaneous and perirenal tissue were comparable (P>0.05), and both contained more (P<0.05) myristic acid than was found in intramuscular tissue. Tissue differences within sheep were all different from each other, with subcutaneous having the greatest (P<0.05) amount, followed by perirenal tissue, with intramuscular tissue containing the least (P<0.05) myristic acid (Fig. 5.2.).

Table 5.1. Main effects of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison and sheep finished on forage

Fatty Acid			Species			Tissue				Effect
			Bison	Sheep	P SEM	Subcutaneous	Perirenal	Intramuscular	P SEM	
			mg g^{-1} total fatty acid methyl esters							
14:0		Myristic	27.66	90.35	0.90	71.79	63.37	41.86	1.65	*c*
14:1	*c*-9	Myristoleic	2.11	3.99	0.11	2.54	0.91	5.71	0.20	*c*
15:0		Pentadecanoic	23.06	9.94	2.54	10.88	8.64	29.97	4.65	*c*
16:0		Palmitic	220.34	263.51	3.34	260.29	244.20	221.28	6.11	*c*
16:1	*c*-9	Palmitoleic	26.01 d	21.32 e	0.93	29.34 d	22.11 e	19.55 e	1.70	*ab*
17:0		Margaric	26.77 d	16.84 e	1.44	19.96	23.41	22.06	2.64	*a*
17:1	*c*-9	Heptadecenoic	3.60	4.18	0.19	3.92 e	2.44 f	5.31 d	0.34	*b*
18:0		Stearic	220.74	156.78	4.06	165.10	269.52	131.66	7.44	*c*
18:1	*t*-9	Elaidic	4.60	4.00	0.61	5.13	3.19	4.59	1.12	
18:1	*t*-11	Transvaccenic	41.54	30.67	2.06	40.12	46.48	21.71	3.78	*c*
18:1	*c*-9	Oleic	287.62 e	334.59 d	8.22	339.30 d	267.47 e	326.56 d	15.04	*ab*
18:1	*c*-11	Vaccenic	11.51 d	4.27 e	0.65	4.57 e	3.65 e	15.46 d	1.20	*ab*
18:2	*c*-9,12	Linoleic	48.72	19.70	4.28	17.20	17.33	68.10	7.84	*c*
20:0		Arachidic	2.69 d	1.94 e	0.13	2.06 e	3.85 d	1.04 f	0.24	*ab*
18:3	*c*-6,9,12	γ-Linolenic	0.29	0.22	0.03	0.10	0.09	0.58	0.06	*c*
20:1	*c*-11	Eicosenoic	0.67	0.18	0.20	0.62	0.31	0.35	0.37	
18:3	*c*-9,12,15	α-Linolenic	18.62 d	12.55 e	1.36	10.98 e	11.51 e	24.27 d	2.49	*ab*
18:2	*c*-9,*t*-11	CLA	5.79	13.10	0.24	11.55 d	7.79 f	8.99 e	0.44	*ab*
18:2	*t*-10,*c*-12	CLA	0.03	0.00	0.02	0.00	0.01	0.04	0.03	
20:2	*c*-11,14	Eicosadienoic	0.47	0.60	0.06	0.22 e	0.15 e	1.24 d	0.11	*b*
22:0		Behenic	0.27	0.12	0.03	0.06	0.01	0.50	0.05	*c*
20:3	*c*-8,11,14	Homo-γ-linolenic	1.83	0.66	0.16	0.42	1.01	2.31	0.29	*c*
20:3	*c*-11,14,17	Eicosatrienoic	0.18	0.13	0.02	0.07 e	0.07 e	0.32 d	0.04	*b*
22:1	*c*-13	Erucic	0.40	0.18	0.05	0.21	0.18	0.48	0.08	*c*
20:4	*c*-5,8,11,14	Arachidonic	12.73	4.52	1.29	0.81	0.61	24.46	2.36	*c*
22:2	*c*-13,16	Docosadienoic	0.51 d	0.15 e	0.10	0.18	0.17	0.64	0.18	*a*
20:5	*c*-5,8,11,14,17	Eicosapentaenoic	2.62	0.98	0.36	0.20	0.12	5.07	0.65	*c*
22:4	*c*-7,10,13,16	Docosatetraenoic	0.72	0.26	0.06	0.15	0.07	1.26	0.12	*c*
22:5	*c*-7,10,13,16,19	Docasapentaenoic	6.14	3.27	0.74	1.81	1.18	11.13	1.36	*c*
22:6	*c*-4,7,10,13,16,19	Docosahexaenoic	1.71	0.99	0.25	0.42	0.16	3.47	0.46	*c*

a-b , means within main effect differ (P <0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (P <0.05), shown on Table 5.2.
d-f, means within a row are different (P <0.05) for each main effect.
[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=19; sheep subcutaneous and perirenal, n=3; intramuscular, n=2.

Table 5.2. Interaction effects (*P* <0.05) of subcutaneous, perirenal, and intramuscular adipose tissue samples taken from bison and sheep finished on forage

			Bison[z]			Sheep[z]			
			Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
Fatty Acid			mg g^{-1} total fatty acid methyl esters						
14:0		Myristic	34.37	34.49	14.12	109.22	92.24	69.60	2.33
14:1	*c* -9	Myristoleic	1.58	0.55	4.21	3.49	1.27	7.20	0.28
15:0		Pentadecanoic	11.98	8.94	48.26	9.79	8.35	11.67	6.59
16:0		Palmitic	242.02	240.03	178.96	278.56	248.38	263.59	8.66
18:0		Stearic	212.05	323.61	126.56	118.15	215.42	136.77	10.54
18:1	*t* -11	Transvaccenic	50.84	57.38	16.39	29.40	35.58	27.02	5.35
18:2	*c* -9,12	Linoleic	17.18	17.19	111.79	17.23	17.46	24.41	11.11
18:3	*c* -6,9,12	γ-Linolenic	0.03	0.07	0.78	0.17	0.11	0.37	0.08
22:0		Behenic	0.00	0.00	0.80	0.13	0.03	0.21	0.07
20:3	*c* -8,11,14	Homo-γ-linolenic	0.60	1.30	3.59	0.23	0.72	1.02	0.41
22:1	*c* -13	Erucic	0.20	0.21	0.78	0.21	0.16	0.19	0.12
20:4	*c* -5,8,11,14	Arachidonic	0.79	0.84	36.55	0.83	0.38	12.36	3.34
20:5	*c* -5,8,11,14,17	Eicosapentaenoic	0.19	0.16	7.52	0.21	0.09	2.63	0.93
22:4	*c* -7,10,13,16	Docosatetraenoic	0.13	0.05	1.97	0.16	0.09	0.54	0.17
22:5	*c* -7,10,13,16,19	Docasapentaenoic	1.35	0.89	16.19	2.26	1.47	6.06	1.92
22:6	*c* -4,7,10,13,16,19	Docosahexaenoic	0.13	0.03	4.96	0.71	0.28	1.97	0.65

[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=19; sheep subcutaneous and perirenal, n=3; intramuscular, n=2.

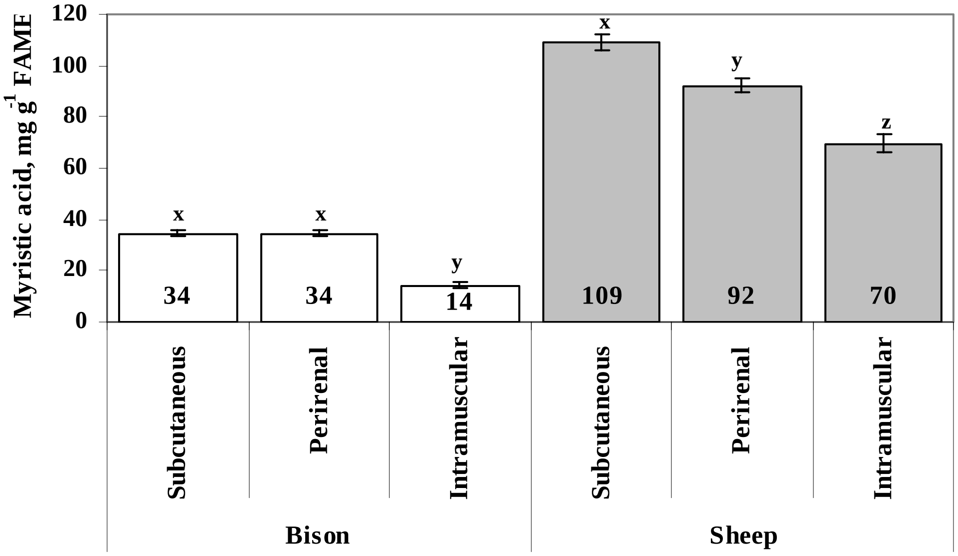

Figure 5.1. Species x tissue type interaction for myristic acid (C14:0), means separation for tissue type within species under forage finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =1.14, sheep =3.10.

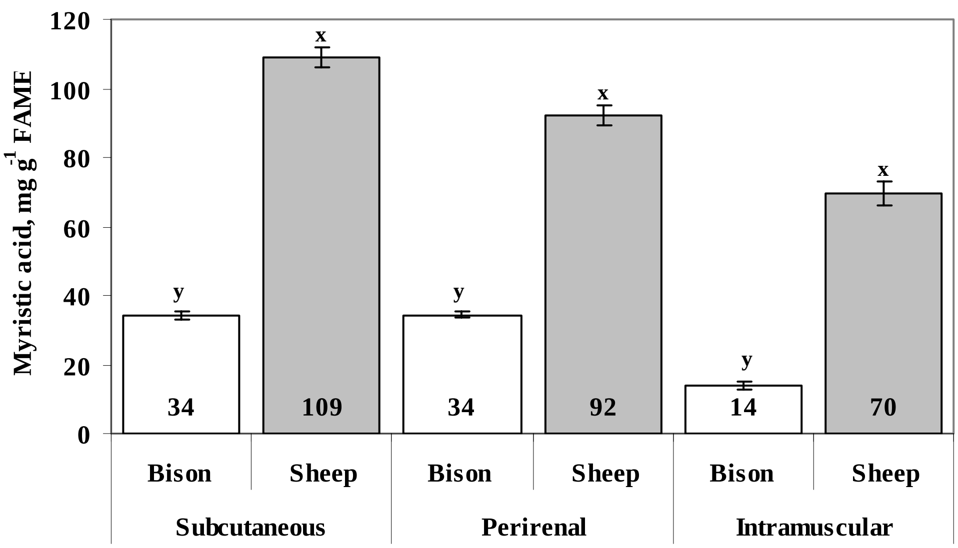

Figure 5.2. Species x tissue type interaction for myristic acid (C14:0), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =1.14, sheep =3.10.

16:0 Palmitic

The interaction effect (*P*<0.05) between tissue types and species for palmitic acid are presented in Table 5.2.. Separation of simple effects (*P*<0.05) for species within tissue types were observed only in intramuscular tissue, where sheep contained more (*P*<0.05) palmitic acid than bison (Fig 5.3.). Separation of simple effects (*P*<0.05) for tissue within species were found only in bison, where there was more (*P*<0.05) palmitic acid in subcutaneous and perirenal tissue than in intramuscular tissue.

Minor C14 to C17 Fatty Acids

Minor fatty acids identified of chain length 14 to 17 include: myristoleic, pentadecanoic, palmitoleic, margaric, and heptadecenoic acid.

The interaction effect (*P*<0.05) between species within tissue type for myristoleic acid (Table 5.2.) showed the content was greater (*P*<0.05) in sheep compared to bison for both subcutaneous and intramuscular tissue. Separation of simple effects (*P*<0.05) showed that in both bison and sheep, intramuscular tissue had a greater (*P*<0.05) amount of myristoleic acid, followed by subcutaneous, with perirenal tissue having the least (*P*<0.05) (Table 5.2.).

The effect (*P*<0.05) of species for palmitoleic acid showed bison to contain more (*P*<0.05) than sheep (Table 5.1.). Effect (*P*<0.05) of tissue for palmitoleic acid indicated a higher (*P*<0.05) proportion in subcutaneous tissue than in either perirenal or intramuscular tissue (Table 5.1.).

Of the odd-chained fatty acids, an interaction effect (*P*<0.05) between species and tissue type was observed in intramuscular tissue for pentadecanoic acid (Table 5.2.). In intramuscular tissue, more (*P*<0.05) pentadecanoic acid was found in bison than in sheep. Only in bison were there tissue differences, as shown by a higher (*P*<0.05) proportion of pentadecanoic acid in intramuscular tissue than in subcutaneous or perirenal tissue (Table 5.2.).

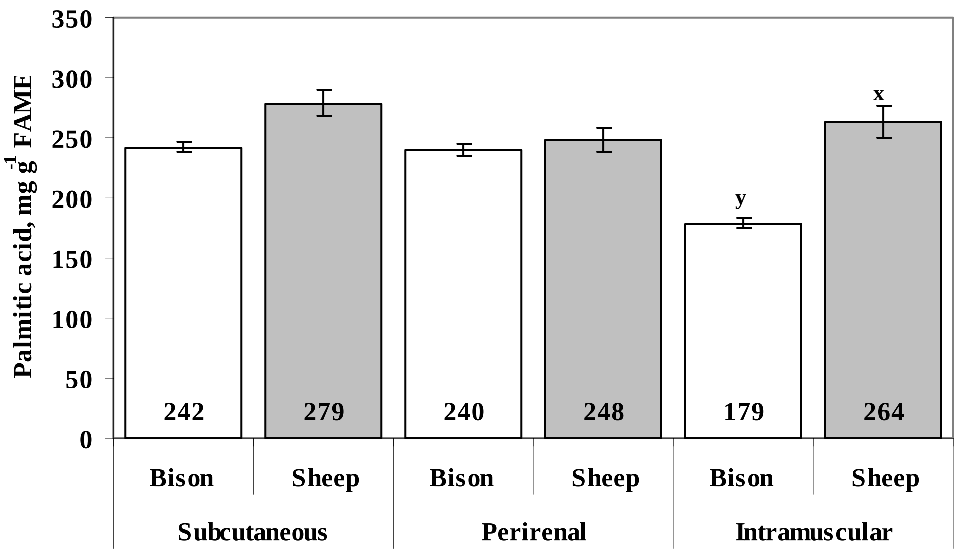

Figure 5.3. Species x tissue type interaction for palmitic acid (C16:0), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05).
Pooled SEM for bison =4.23, sheep =11.50.

Effects (*P*<0.05) of species for margaric acid content show bison to have a greater (*P*<0.05) amount than found in sheep (Table 5.1.).

Effects (*P*<0.05) of tissue type were apparent for heptadecenoic acid, with the largest (*P*<0.05) amount being found in intramuscular tissue, followed by subcutaneous tissue, with perirenal tissue containing the least (*P*<0.05) (Table 5.1.).

5.3.2. Saturated and Monounsaturated Fatty Acids of C18 Chain Length

18:0 Stearic

Interaction effects (*P*<0.05) were observed between species and tissue types for stearic acid (Table 5.2.). In both subcutaneous and perirenal tissues, bison contained more (*P*<0.05) stearic acid than found in sheep (Fig 5.4.). Evaluation of simple effects (*P*<0.05) of tissue types within bison, showed that tissues differed (*P*<0.05) from each other, with the greatest (*P*<0.05) amount of stearic acid being located in perirenal tissue, followed by subcutaneous tissue, with intramuscular tissue containing the least (*P*<0.05) (Fig. 5.5.). Separation of simple effects (*P*<0.05) for sheep showed that perirenal tissue contained more (*P*<0.05) stearic acid than did either subcutaneous or intramuscular tissue, which were similar (*P*>0.05) (Fig. 5.5.).

18:1 *t*-11 *Trans*vaccenic

An interaction (*P*<0.05) between species and tissue type for *trans*vaccenic acid was observed (Table 5.2.). Evaluations of simple effects (*P*<0.05) indicated that in both subcutaneous and perirenal tissues, bison contained a greater (*P*<0.05) amount of *trans*vaccenic acid than did sheep (Fig. 5.6.). Separation of simple effects (*P*<0.05) for tissue types were only visible in bison, with subcutaneous and perirenal tissue containing larger (*P*<0.05) amounts of *trans*vaccenic acid than did intramuscular tissue.

18:1 *c*-9 Oleic

Effect (*P*<0.05) of tissue type for oleic acid indicated that intramuscular and subcutaneous tissue were similar (*P*>0.05), both having a greater (*P*<0.05) amount than perirenal tissue (Table 5.1.). Species effect (*P*<0.05) showed sheep to have an overall greater (*P*<0.05) oleic content than did bison (Table 5.1.).

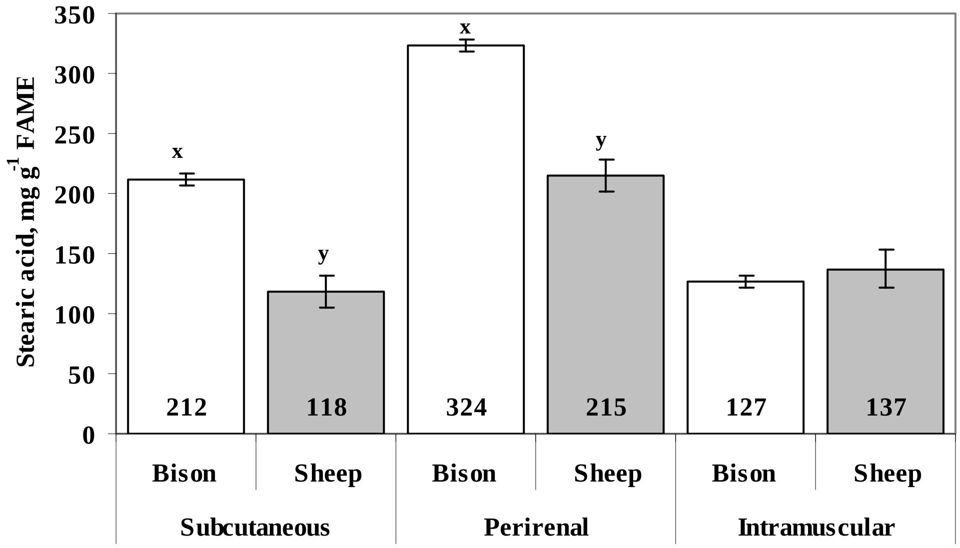

Figure 5.4. Species x tissue type interaction for stearic acid (C18:0), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for bison = 5.14, sheep =19.98.

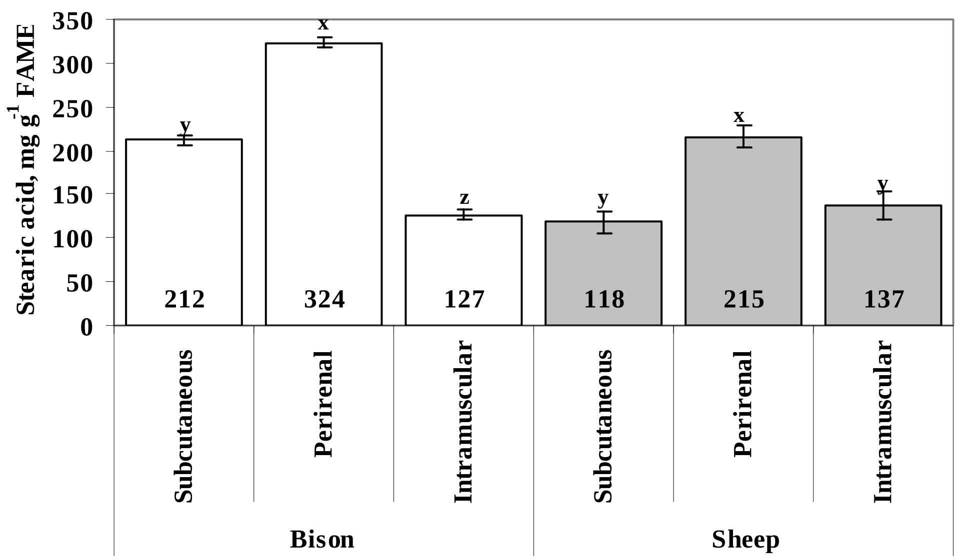

Figure 5.5. Species x tissue type interaction for stearic acid (C18:0), means separation for tissue type within species under forage finishing conditions. Means within species followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for bison =5.14, sheep =19.98.

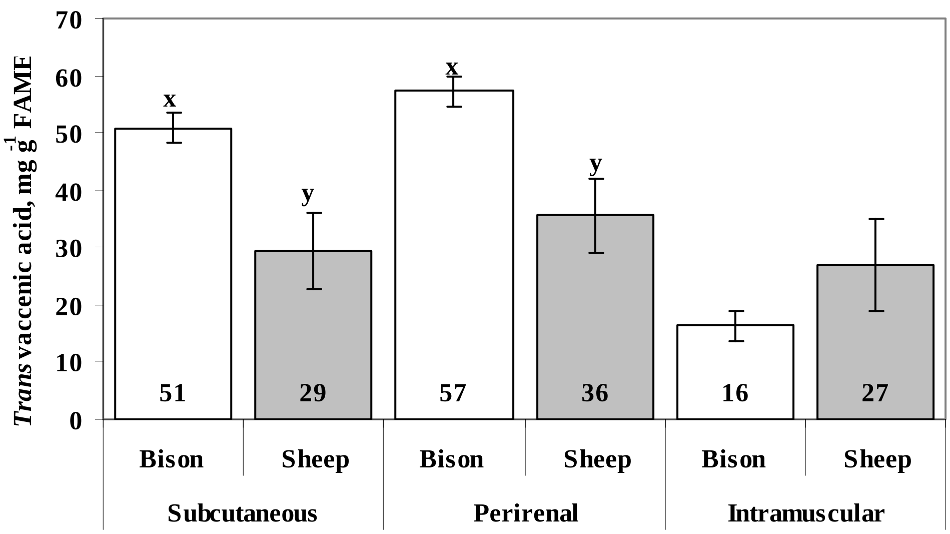

Figure 5.6. Species x tissue type interaction for *trans* vaccenic acid (C18:1, *t*-11), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =2.61, sheep =7.11.

Of the minor fatty acids identified in the C18 monounsaturated range, which included elaidic and vaccenic acid, only differences in the amount of vaccenic acid were observed. Effect ($P<0.05$) of tissue showed greater ($P<0.05$) amounts of vaccenic acid in intramuscular tissue than in subcutaneous or perirenal tissue (Table 5.1.). Effect of species showed bison to have a greater ($P<0.05$) content of vaccenic acid than did sheep (Table 5.1.).

5.3.3. C18 Diunsaturated, Conjugated Linoleic Acid and Polyunsaturated

18:2 *c*-9, 12 Linoleic

An interaction effect ($P<0.05$) was observed between species and tissue types for linoleic acid (Table 5.2.). Separation of simple effects ($P<0.05$) showed bison containing more ($P<0.05$) linoleic acid than sheep within intramuscular tissue (Fig 5.7.). Separation of simple effects ($P<0.05$) for tissues within species showed that the intramuscular tissue of bison had a larger ($P<0.05$) proportion of linoleic acid than did either subcutaneous or perirenal tissue (Table 5.2.).

18:3 α-Linolenic

Effect ($P<0.05$) of species for α-linolenic acid content indicated bison contained more ($P<0.05$) α-linolenic acid than sheep (Table5.1). Effect ($P<0.05$) of tissue type indicate a higher proportion to be located in intramuscular tissue than in subcutaneous or perirenal tissue (Table 5.1.).

Conjugated Linoleic Acid Isomers

Effect ($P<0.05$) of species for the conjugated linoleic isomer C18:2 *c*-9, *t*-11 was found to be greater ($P<0.05$) in sheep than in bison (Table 5.1.). Effect ($P<0.05$) for tissue type showed there was a greater ($P<0.05$) accumulation of CLA *c*-9, *t*-11 in subcutaneous tissue than in the perirenal or intramuscular tissue (Table 5.1.).
Minor amounts of the CLA *t*-10, *c*-12 isomer were detected in bison and sheep tissues; however, no species or tissue differences were identified.

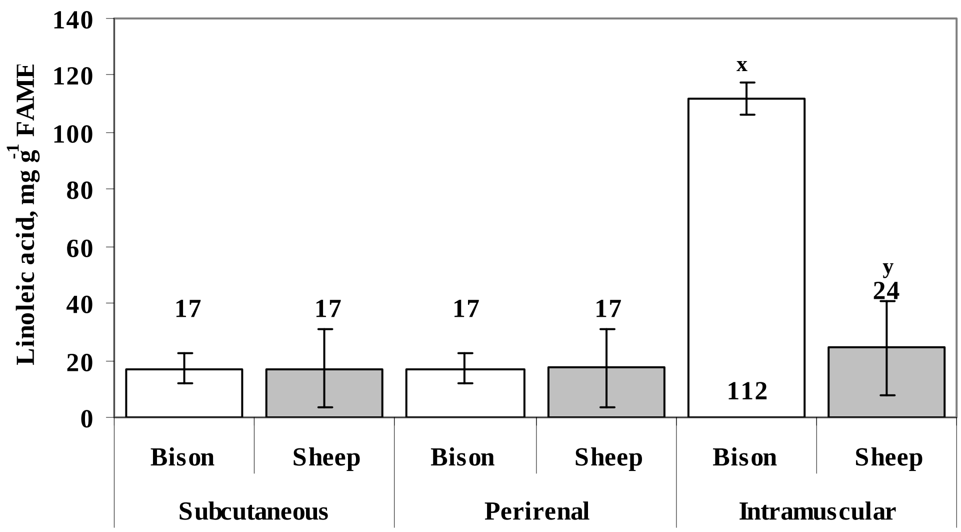

Figure 5.7. Species x tissue type interaction for linoleic acid (C18:2 *c* -9, 12), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =5.42, sheep =14.74.

Minor C18 Polyunsaturated Fatty Acids

An interaction effect (P<0.05) was identified between species and tissue types for the minor amounts of γ-linolenic acid detected in intramuscular tissues (Table 5.2.). Separation of simple effects (P>0.05) for species within tissue types indicated more (P<0.05) γ-linolenic acid could be found in bison than in sheep. Separation of simple effects (P<0.05) within tissue type was apparent only in the bison group, with bison intramuscular tissue containing a larger (P<0.05) proportion of γ-linolenic than did subcutaneous or perirenal tissue.

5.3.4. Saturated and Unsaturated Fatty Acids of C20 to C22 Chain Length

20:4 Arachidonic

There was an interaction (P<0.05) between species and tissue type for arachidonic acid. Separation of simple effects (P<0.05) for species within tissue types showed only intramuscular tissue having a species effect, with bison having a greater (P<0.05) amount of arachidonic acid than sheep (Fig. 5.8.). Simple effects (P<0.05) for tissue within species for arachidonic acid indicated bison had a greater (P<0.05) accumulation in intramuscular tissue than in subcutaneous or perirenal tissue.

20:5 Eicosapentaenoic

The interaction (P<0.05) between species and tissue types was visible for eicosapentaenoic acid (Table 5.2.). Simple effects (P<0.05) showed bison contained a larger (P<0.05) proportion of eicosapentaenoic acid in the intramuscular tissue than didsheep (Fig. 5.9.). Tissue differences within species were observed only in bison (Table 5.2.). Separation of simple effects (P<0.05) for bison showed that intramuscular tissue contained larger (P<0.05) amounts of eicosapentaenoic acid than either subcutaneous or perirenal tissue, which were similar (P>0.05).

22:5 Docosapentaenoic

An interaction (P<0.05) between species and tissue types was observed for docosapentaenoic acid (Table 5.2.). Simple effects (P>0.05) of species within intramuscular tissue showed bison containing more (P<0.05) docosapentaenoic acid

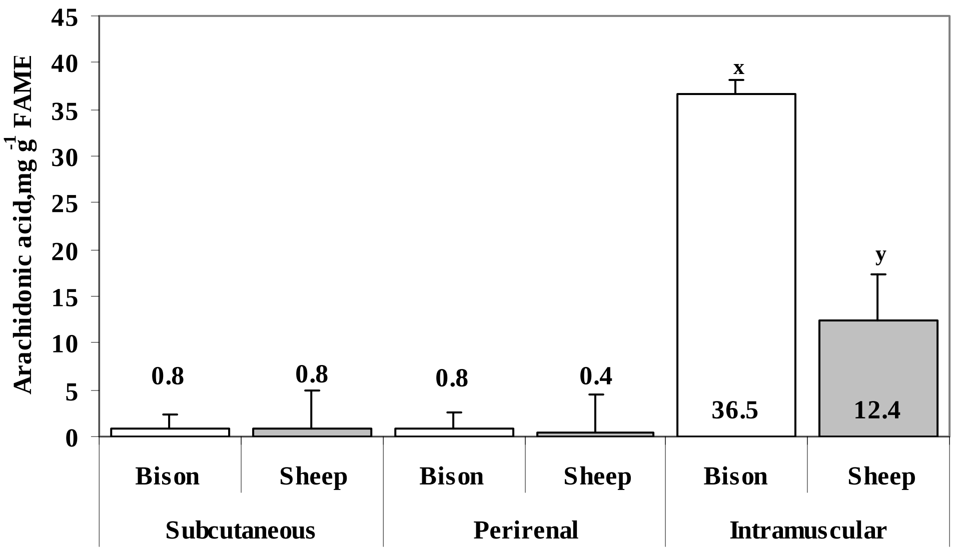

Figure 5.8. Species x tissue type interaction for arachidonic acid (C20:4), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05).
Pooled SEM for bison =1.63, sheep =4.43.

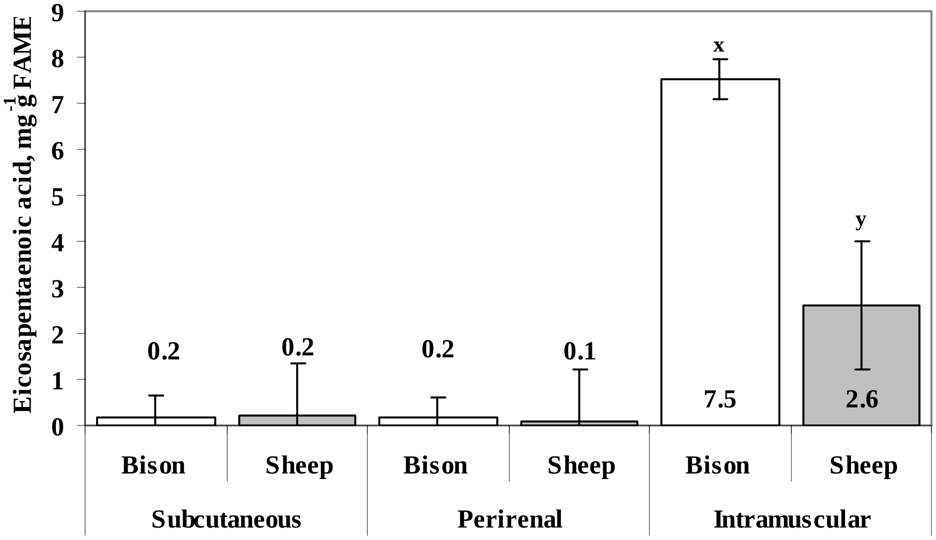

Figure 5.9. Species x tissue type interaction for eicosapentaenoic acid (C20:5), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.45, sheep =1.23.

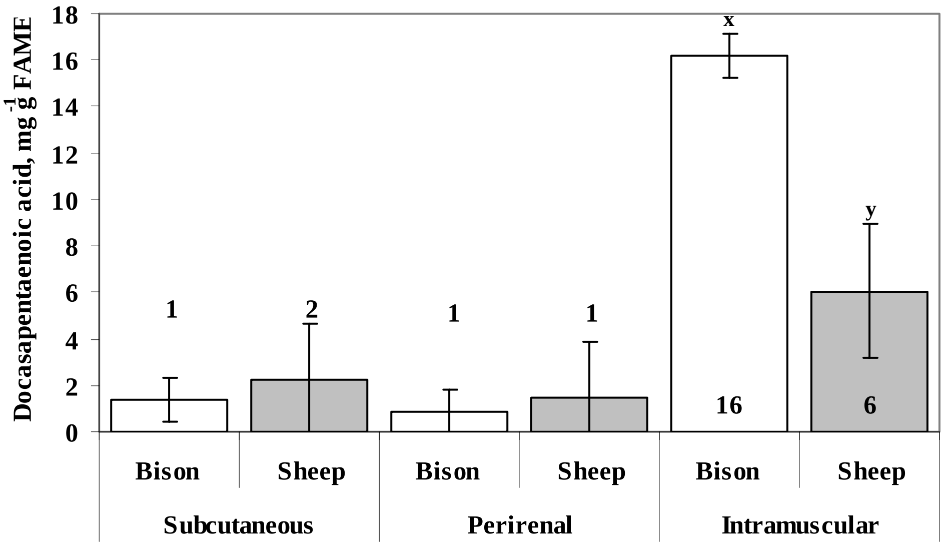

Figure 5.10. Species x tissue type interaction for docasapentaenoic acid (C22:5), means separation for species within tissue type under forage finishing conditions. Means within tissue followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =0.94, sheep =2.55.

than sheep (Fig. 5.10.). Simple effect separations ($P<0.05$) for tissue differences within species were shown for bison, with intramuscular tissue containing a larger ($P<0.05$) proportion of docosapentaenoic acid than either subcutaneous or perirenal tissue.

22:6 Docosahexaenoic

An interaction ($P<0.05$) between species and tissue types was observed for docosahexaenoic acid (Table 5.2.). Simple effects ($P<0.05$) of species within intramuscular tissue showed that bison contained larger ($P<0.05$) proportions of docosahexaenoic acid than did sheep (5.11). Simple effects ($P<0.05$) of tissue within bison showed that intramuscular tissue had more ($P<0.05$) docosahexaenoic acid than either subcutaneous or perirenal tissue (Table 5.2.).

Minor C20 to C22 Fatty Acids

Minor saturated fatty acids identified in the C20:0 to C22:0 range included arachidic and behenic acid. Effect ($P<0.05$) of tissue type (Table 5.1.) showed all three to be different, with perirenal tissue containing the largest ($P<0.05$) proportion of arachidic acid, followed by subcutaneous tissue, with intramuscular tissue containing the least ($P<0.05$). Effect ($P<0.05$) of species showed bison containing greater ($P<0.05$) amounts of arachidic acid than sheep (Table 5.1.).

There was an interaction effect ($P<0.05$) between species and tissue type for behenic acid (Table 5.2.). In intramuscular tissue, evaluation of simple effects ($P<0.05$) show bison contained more ($P<0.05$) behenic acid than did sheep. Separation of simple effects ($P<0.05$) for tissues within species for behenic acid was apparent only in bison tissues, where intramuscular tissue contained more ($P<0.05$) than the other tissues.

Minor monounsaturated fatty acids identified in the C20:0 to C22:0 range included eicosenoic and erucic acid. An interaction effect ($P<0.05$) between species and tissue type was visible only in intramuscular tissue, with bison having a greater ($P<0.05$) amount than did sheep. Separation of simple effects ($P<0.05$) of tissue type within species was identified only in bison, with intramuscular tissue having a greater ($P<0.05$) accumulation of eicosenoic acid than subcutaneous or perirenal tissue. No differences were noted in species or tissue type for eicosenoic acid.

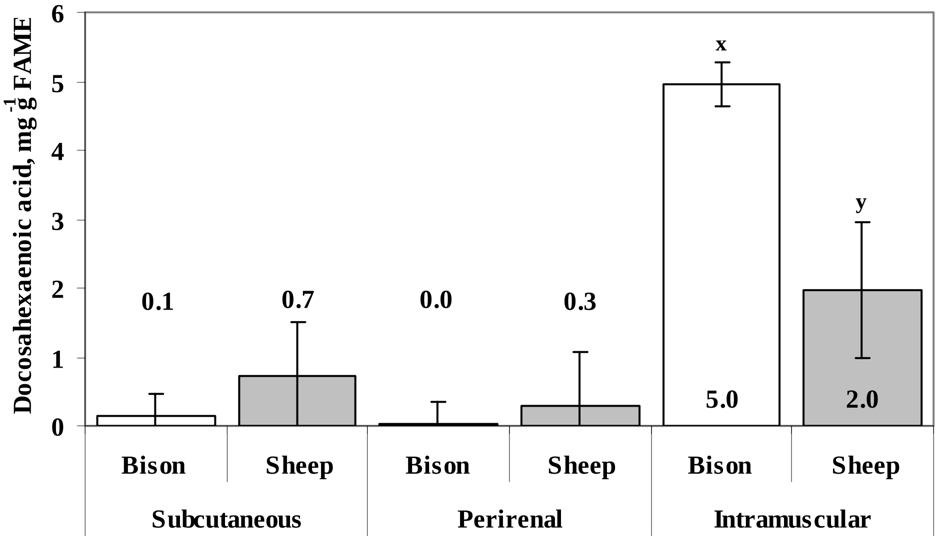

Figure 5.11. Species x tissue type interaction for docosahexaenoic acid (C22:6), means separation for species within tissue type under forage finishing conditions. means within tissue followed by different letters (x,y,z) are different ($P < 0.05$). Pooled SEM for bison =0.32, sheep =0.87.

Minor polyunsaturated fatty acids identified in the C20:0 to C22:0 range included: eicosadienoic, homo-γ-linolenic, eicosatrienoic, docosadienoic, and docosatetraenoic acid. Effects (*P*<0.05) of tissue type were identified for eicosadienoic acid with more (*P*<0.05) being found in intramuscular tissue than in subcutaneous or perirenal tissue (Table 5.1.).

A species by tissue type interaction (*P*<0.05) for homo-γ-linolenic acid was found in intramuscular tissue and separation of simple effects (*P*<0.05) indicated a greater (*P*<0.05) amount in bison than in sheep. Separation of simple effects (*P*<0.05) for tissue types within species were found in bison only, where a greater (*P*<0.05) amount of homo-γ-linolenic acid was found in intramuscular tissue than in subcutaneous or perirenal tissue.

Effect (*P*<0.05) of tissue type for eicosatrienoic acid showed a greater (*P*<0.05) amount in intramuscular tissue than in subcutaneous or perirenal tissue (Table 5.1.)

Effect (*P*<0.05) of species for docosadienoic acid showed a larger (*P*<0.05) amount in bison than in sheep (Table 5.1.).

Interaction (*P*<0.05) between species and tissue type for docosatetraenoic acid showed bison to have a greater (*P*<0.05) content than sheep in intramuscular tissue (Table 5.2.). Separation of simple effects (*P*<0.05) of tissues within species were apparent only in bison, with intramuscular tissue containing greater (*P*<0.05) amounts of docosatetraenoic acid than did subcutaneous or perirenal tissue.

5.3.5. Fatty Acid Totals and Selected Ratios

Interaction (*P*<0.05) effects for all of the selected fatty acid totals and ratios are presented in Table 5.4.. There was a species by tissue interaction (*P*<0.05) for total saturated fatty acid (SFA) content in intramuscular tissue. Separation of simple effects (*P*<0.05) showed that within intramuscular tissue, sheep contained a greater (*P*<0.05) amount of total SFA than did bison. Separations of simple effects (P<0.05) for tissue types were observed for bison and sheep (Table. 5.2). Within bison, tissues were all different (*P*<0.05) from each other, with perirenal tissue having the greatest

Table 5.3. Main effects for total fatty acid groups for species and tissue samples from bison and sheep finished on forage

Fatty Acid Group	Species[z] Bison	Sheep	P SEM	Tissue[z] Subcutaneous	Perirenal	Intramuscular	P SEM	Effect
	mg g^{-1} total fatty acid methyl esters							
SFA	521.53	539.48	5.25	530.15	613.00	448.37	9.61	*c*
PUFA	100.37	57.12	7.82	44.12	40.27	151.85	14.32	*c*
PUFA/SFA[y]	0.23	0.11	0.02	0.08	0.07	0.36	0.04	*c*
ω-3[x]	29.28 a	17.91 b	2.56	13.48 a	13.05 a	44.25 b	4.68	*ab*
ω-6[w]	83.09	38.30	6.69	29.77	30.68	121.62	12.23	*c*
ω-6/ω-3	2.73	2.20	0.22	2.25	2.38	2.76	0.39	

a-b , means within main effect differ (P <0.05); *a* = treatment effect, *b* = tissue effect; *c* = species x tissue interaction (P <0.05), shown on Table 5.4.

d-f, means within a row are different (P <0.05) for each main effect.

[z] sample numbers for bison, n=19; sheep, n=3; subcutaneous and perirenal, n=22; intramuscular, n=21.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-3 fatty acids include 18:3 *cis* -9,12,15, 20:3 *cis* -11,14,17, 20:5 *cis* -5,8,11,14,17, 22:5 *cis* -7,10,13,16,19, 22:6 *cis* -4,7,10,13,16,19.

[w] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 cis-5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

Table 5.4. Interaction effects (*P* <0.05) for total fatty acid groups for species and tissue samples from bison and sheep finished on forage

	Bison[z]			Sheep[z]			
	Subcutaneous	Perirenal	Intramuscular	Subcutaneous	Perirenal	Intramuscular	P SEM
	mg g^{-1} total fatty acid methyl esters						
SFA	547.16	659.30	401.38	557.58	606.02	495.51	13.62
PUFA	40.91	38.50	221.69	47.33	42.03	82.01	20.29
PUFA/SFA[y]	0.07	0.06	0.55	0.08	0.07	0.17	0.05
ω-6[x]	18.97	19.57	155.73	18.82	18.94	40.15	17.34

[z] sample numbers for bison subcutaneous, perirenal, and intramuscular tissue, n=19; sheep subcutaneous and perirenal tissue, n=3; intramuscular tissue, n=2.

[y] PUFA/SFA is the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA).

[x] ω-6 fatty acids include 18:2 *cis* -9,12, 18:3 *cis* -6,9,12, 20:2 *cis* -11,14, 20:3 *cis* -8,11,14, 20:4 *cis* -5,8,11,14, 22:2 *cis* -13,16, and 22:4 *cis* -7,10,13,16.

proportion of SFA, followed by subcutaneous tissue, with intramuscular tissue containing the least (Fig. 5.12.). Within sheep, perirenal tissue contained the most (P<0.05) SFA, with subcutaneous and intramuscular tissue containing similar amounts (Fig 5.12.).

Although species differences were present only in intramuscular tissue, sheep contained only 37% of the level of polyunsaturated fatty acid (PUFA) located in bison intramuscular tissue. Interactions (P<0.05) of tissue type by species were noted in bison, with intramuscular tissue containing more (P<0.05) PUFA than either subcutaneous or perirenal tissue (Table 5.4.).

There was an interaction effect (P<0.05) between species and tissue types for the ratio of PUFA to SFA. Separation of simple effects (P<0.05) for species showed that within intramuscular tissue, bison had a greater (P<0.05) ratio than that of sheep. Separation of simple effects (P<0.05) for tissue type by species show bison intramuscular tissue had a higher (P<0.05) ratio of PUFA to SFA than did subcutaneous or perirenal tissue.

Effect (P<0.05) of tissue type for omega-3 fatty acids (Table 5.3.) indicated a greater (P<0.05) proportion accumulating in intramuscular tissue than in subcutaneous or perirenal tissue, which were similar (P>0.05). Effect (P<0.05) of species show bison to have a larger (P<0.05) proportion of omega-3 fatty acids than sheep (Fig. 5.13.), (Table 5.3.).

An interaction effect (P<0.05) between species and tissue types for total omega-6 fatty acid content were apparent ((Table 5.4.). Separation of simple effects (P<0.05) within intramuscular tissue showed bison contained a higher (P<0.05) proportion of omega-6 fatty acids than sheep in intramuscular tissue. Separation of simple effects (P<0.05) for tissue types within species (Table 5.4.) showed that within bison tissues, intramuscular tissue contained a larger (P<0.05) proportion of omega-6 fatty acids than either subcutaneous or perirenal tissue (Fig. 5.14.).

The ratio of omega-6 to omega-3 fatty acids was similar (P>0.05) for both bison and sheep at 1.78 and 1.47 respectively (SEM 0.56).

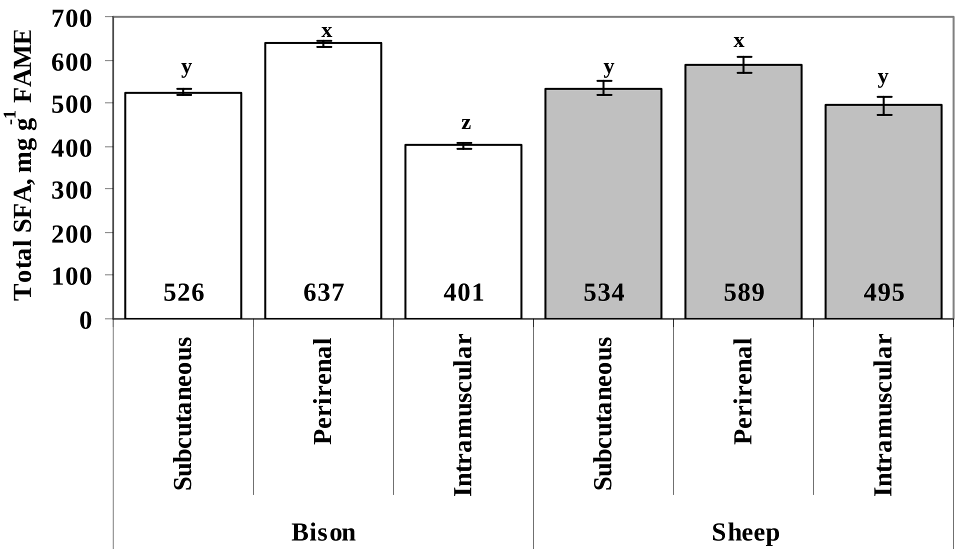

Figure 5.12. Species x tissue type interaction for total saturated fatty acids, means separation for tissue type within species under forage finishing conditions. Means within species followed by different letters (x,y,z) are different (*P* <0.05). Pooled SEM for bison =6.65, sheep =18.08.

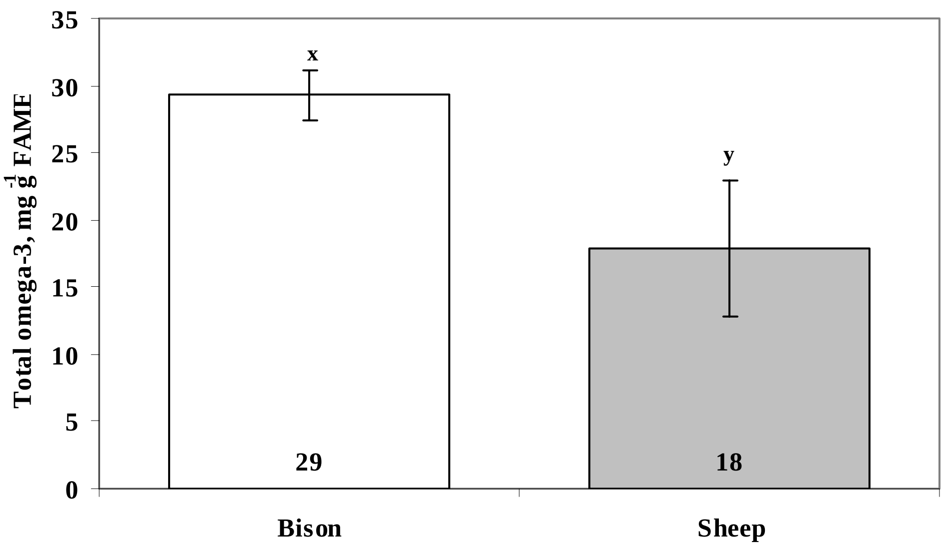

Figure 5.13. Effect of species on the total omega-3 fatty acids in forage fed bison and sheep. Means within species followed by different letters (x,y) are different (*P* <0.05). SEM for bison =1.87, sheep =5.08.

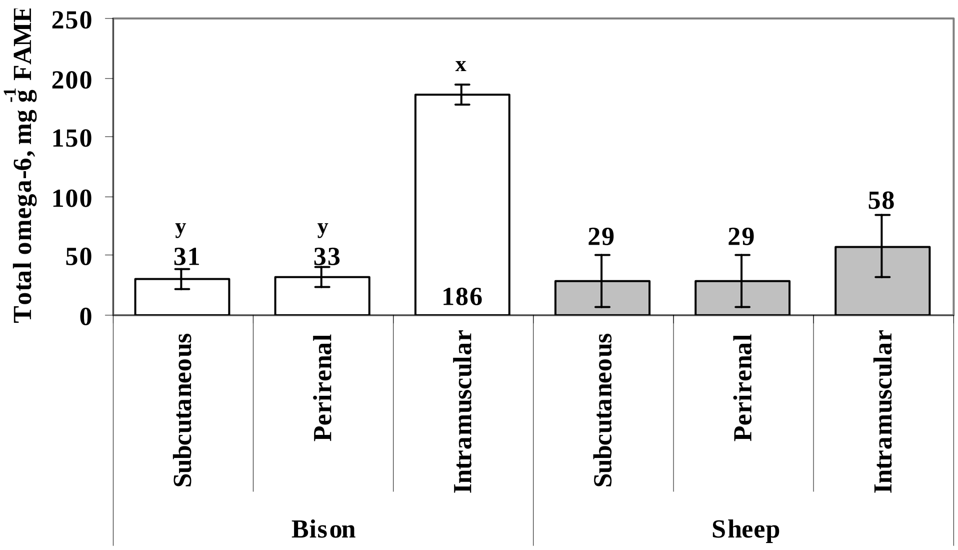

Figure 5.14. Species x tissue type interaction for total omega-6 fatty acids, means separation for tissue type within species under forage finishing conditions. Means within species followed by different letters (x,y,z) are different (P <0.05). Pooled SEM for bison =8.46, sheep =23.01.

5.4. Discussion

The samples collected from animals within this study are typical of those found under commercial conditions, and are representative of the forage finished bison and sheep industry within Saskatchewan. Commercial producers representing the two species supplied the tissue samples for this study. Factors such as forage composition, time of slaughter, and age of the animal at the time of slaughter were all decisions made by the individual producer, making feed intake and nutrient composition of the diet impossible to control or record. Information gathered during the study provides a one time look at the fatty acid profile of bison and sheep tissues produced under commercial forage finishing conditions.

Tissues of ruminant animals tend to contain large amounts of saturated fatty acids as a consequence of the *de novo* synthesis of myristic and palmitic acids and extensive biohydrogenation of linoleic and linolenic acids in the rumen. Increased content of SFA in human diets is often linked to a rise in the total cholesterol level and are associated with an increased amount of low density lipoproteins in the blood stream. The presence of SFA within tissues in the form of triacylglycerides is a reflection of the level of SFA found in the diet or a product of digestion, and are most often associated with storage adipose tissue rather than membrane tissues (Rhee 2000). The higher content of SFA found in perirenal tissue rather than subcutaneous tissue could be an evolutionary response to seasonal temperature differences both species would encounter. Finding almost 20% more SFA present in sheep intramuscular tissue than in bison intramuscular tissue can be explained by the presence of intramuscular deposits, or marbling, which was not visible in the bison intramuscular tissue.

Sheep had only 37% of the PUFA content of bison within intramuscular tissue, but no differences between sheep or bison were observed for the other tissues. Polyunsaturated fatty acids are generally 18-carbons long or greater and are most often associated with phospholipids due to the specificity of the acyl-transferase. Very little PUFA is encountered in subcutaneous or perirenal tissues as the majority of these lipid storage sites, as with all fat deposits, are comprised of triacylglycerides surrounded by a thin membrane layer. However, muscle tissue contains considerable portions of PUFA in the membrane bilayer, aiding in cell fluidity. The absence of visible amounts of marbling within the bison ribeye tissue coupled with the higher content of PUFA observed in bison intramuscular tissue is a testament to the degree in which marbling influences the fatty acid profile of the tissue. The lower content of PUFA found in sheep intramuscular tissue could be explained by a dilution effect caused by marbling within the tissue. The degree of marbling present in the two species could be a result of genetic differences, but most likely was a result of the physiological age and degree to which each animal was finished.

The differences observed between bison and sheep in PUFA to SFA ratio were present in intramuscular tissue only, and there was a more than three-fold difference between species, which is not surprising given the observations for the amount of PUFA in each species. The greater proportion of linoleic acid found in bison intramuscular tissue accounts for much of the difference observed between the bison and sheep intramuscular ratios. Within the intramuscular tissue, bison had more than 4.5 times the amount of linoleic acid as did sheep. Equivalent amounts of stearic acid were found in both bison and sheep intramuscular tissue. Therefore, differences in the SFA content would be reliant on the content of myristic and palmitic acids found in the intramuscular tissue, which are more of a concern from a human health perspective. Such observed differences in amounts of myristic acid present in the tissues would indicate a more active elongase activity in the bison tissue. In that bison have one fifth of the myristic acid in intramuscular tissue compared to sheep, it could be postulated that myristic acid is only a temporary state in the elongation process to palmitic acid in bison, whereas sheep may store more myristic acid in triacylglyceride form.

Differences between tissues for palmitic acid content were negligible, except in the case of intramuscular tissue. The 32% greater amount of palmitic acid present in sheep intramuscular tissue can be explained by an observable amount of marbling being present within the tissue. The amount of marbling again could be a reflection of the animals physiological maturity and the degree of finish the animal achieved prior to slaughter.

Odd chain fatty acids such as pentadecanoic and margaric are most likely the end result of elongation from a propionate precursor. Accumulation of odd chain fatty acids has been attributed to a deficiency of vitamin B_{12} in the system (Whetsell et al.

2004). Other studies using beef have shown an increased content of branched chain fatty acids in animals finished on forage. There may be microbial factors unique to each species which could cause greater production of propionate within bison rumen fermentation. For both pentadecanoic and margaric acid, bison contained greater amounts in its tissues than did sheep. Within bison, intramuscular tissue accumulated the odd chain fatty acids rather than the depot sites.

Although oleic acid makes up roughly a third of the fatty acids identified in tissues of both species, it is regarded as neutral in its effect on cholesterol levels in humans. The oleic acid content of bison was 86% that of sheep. With both species, greater amounts of oleic acid were found in subcutaneous and intramuscular tissue as compared to perirenal tissue. The fact that more monounsaturated fatty acid was located in intramuscular and subcutaneous tissue reaffirms findings from the literature stating that there is an increased degree of unsaturation the further the tissue is from the body core (Rhee 2000; Marmer et al. 1984; Bolte et al. 2002).

Although mono-*trans*-octadecenoic fatty acids are present only in minor amounts in animal tissue, it should be mentioned that the majority consists of *tran*vaccenic acid, with minor amounts being elaidic acid. Studies on the detrimental effects of *trans*-fatty acids have focused on the impact of partial hydrogenation of plant oils, elaidic acid in particular, and its link to coronary heart disease. Findings have shown that both *trans*-9 and *trans*-10 C18:1 are positively correlated to an increased risk of coronary heart disease, while no such link to *trans*vaccenic acid has been made (Bauman et al. 2004). Studies looking at the link between the intake of mono-*trans*-octadecenoic fatty acids of ruminant origin and the risk of coronary heart disease have noted a negative association (Bauman et al. 2004).

*Trans*vaccenic acid is a common endpoint in the rumen biohydrogenation process for both linoleic and linolenic acids (Harfoot and Hazlewood 1997). The conversion of *trans*vaccenic acid to stearic acid creates a bottleneck as there are currently only two *Fusocillus* bacterial species and a third unnamed bacterial species, R8/5, that are able to perform this function (Harfoot and Hazlewood 1997). As a result of this bottleneck, there is a build-up of *trans*vaccenic acid in the rumen, some of which escapes and is absorbed in the small intestine. This absorbed *trans*vaccenic acid becomes incorporated into the tissues where it can undergo further desaturation into CLA *c*-9, *t*-11. The amount of *trans*vaccenic acid deposited in bison was greater than sheep in subcutaneous and perirenal tissue by 56% and 63% respectively.

The CLA *c*-9, *t*-11 content of bison was only 44% that of sheep. Tissue differences indicated a greater amount in subcutaneous tissue than in perirenal or intramuscular tissue. The amount of *trans*vaccenic acid in the tissues did not seem to relate to the amount of CLA in the tissues. The CLA *c*-9, *t*-11 content was higher for sheep, where as bison had a higher content of *trans*vaccenic acid. Greater desaturase activity was suspected in subcutaneous tissue, as equivalent amounts of *trans*vaccenic acid were present in both subcutaneous and perirenal tissue, yet subcutaneous tissue had a greater content of CLA *c*-9, *t*-11. The least amount of *trans*vaccenic acid detected was in intramuscular tissue for both species; the CLA *c*-9, *t*-11 content of the intramuscular tissue was also low. However, relating the CLA *c*-9, *t*-11 content to the *trans*vaccenic content of the tissue would show intramuscular tissue to have the highest conversion ratio of the three tissues. The high ratio found in intramuscular tissue would indicate it had the most Δ-9 desaturase activity of the three tissues.

The total content of omega-6 fatty acids is a result of linoleic acid intake and subsequent desaturation and elongation within the tissues. Rumen biohydrogenation of linoleic acid is estimated to be in the range of 70 to 95%, with a mean of 80% (Doreau and Ferlay 1994). The linoleic acid content of the intramuscular tissue of bison was four times that of sheep. Linoleic acid that escapes biohydrogenation is incorporated into the tissues being primarily incorporated into the phospholipid layers of the muscle membranes where it undergoes further desaturation. The omega-6 fatty acid content of intramuscular tissue was 5.6 times and 2 times greater than in the other tissues for bison and sheep, respectively. Overall the omega-6 content of bison intramuscular tissue was roughly three times that of sheep tissue. Some of the elongated and desaturated intermediates of linoleic acid act as precursors for eicosanoid production. One of the first intermediates of the desaturase/elongation of linoleic acid is homo-γ-linoleic acid, which acts as a precursor for series-1 prostaglandins. Further desaturation results in the formation of arachidonic acid, which is the most abundant of the PUFAs arising from linoleic acid. Arachidonic acid content was more than three times higher in bison intramuscular tissue than in sheep. Arachidonic acid acts as the precursor for series-2 prostaglandins and series-4 leukotrienes (Calder and Grimble 2002). Eicosanoids derived from omega-6 fatty acids are widely acknowledged to have pro-inflammatory effects on the body's immune response. The inflammation response is a self-preservation action to alleviate the effects of lesions inflicted on the body either by microorganisms, toxins, or allergens, and subsequent secondary consequences caused by the initial disruption (Gil 2002).   Chronic inflammation can be caused by numerous diseases and can lead to an over production of eicosanoids, resulting in long-term detriment to health.

The total content of omega-3 fatty acids results from the sum of α-linolenic acid and all of the long chain polyunsaturated fatty acids derived from α-linolenic. Species differences indicated sheep to have almost 40% lower omega-3 fatty acid content than that of bison. The hypolipidemic effects attributed to omega-3 fatty acids are only applicable to long-chain omega-3 polyunsaturated fatty acids, as α-linolenic acid has been shown to have no effect on triacylglycerol concentrations in the blood (Simopoulos 2000). Increased dietary intake of omega-3 polyunsaturated fatty acids reduces the incidence of coronary heart disease. This action may be independent of any effect these fatty acids have on blood lipid levels (Simon et al. 1995). Based on the findings of this study, intramuscular lipids of ribeye tissue from bison would provide a greater amount of omega-3 fatty acids than an equivalent amount of ribeye tissue from sheep.

The necessity of omega-3 fatty acids for proper neurological development has been well documented (Llanos et al. 2004; Uauy et al. 2001). Early child development of neurological and retinal tissues have been shown to benefit from supplementation with longer chain omega-3 polyunsaturated fatty acids such as docosahexaenoic acid.

The eicosapentaenoic acid content of intramuscular tissue of bison was 2.7 times that of sheep. Eicosapentaenoic acid is a competitive inhibitor of the formation of eicosanoids derived from arachidonic acid (Adam 2004). The actions of the omega-3 fatty acid family are associated with dampening the inflammatory responses brought on by stimulation of the immune system (Gil 2002), as a result of their competitive inhibition of arachidonic acid as precursors for eicosanoids. Intake of one to eight grams of omega-3 fatty acids per day has been shown to reduce the effects of many inflammatory diseases in humans (Gil 2002). Eicosapentaenoic acid promotes the formation of series-3 prostaglandins and series-5 leukotrienes. The conversion of α-linolenic acid to eicosapentaenoic acid is greater in bison than in sheep, in the order of 4.1:1 to 6.8:1, respectively.

Docosapentaenoic acid has been shown to be the most potent inhibitor of blood platelet aggregation compared to its precursor, eicosapentaenoic acid, and its successor, docosahexaenoic acid (Akiba et al. 2000). As an elongase product of EPA, higher levels of DPA were found in bison intramuscular tissue compared to that of sheep intramuscular tissue.

Increased levels of docosahexaenoic acid in the diet have been shown to reduce the risk of coronary heart disease, and to have a positive affect on a number of physiological and psychological disorders. As a desaturase product of DPA, higher levels were found in bison intramuscular tissue compared to sheep intramuscular tissue.

5.5. Summary and Conclusions

Results obtained from comparison of forage finished bison and sheep indicate:

- Total saturated fatty acid content within intramuscular tissue was greater in sheep than in bison, but was similar for subcutaneous and perirenal tissue.
- Both myristic and palmitic acid content were greater in sheep intramuscular tissue than in bison.
- Bison contained a greater proportion of stearic acid within perirenal and subcutaneous tissue, but was similar to sheep in the intramuscular tissue.
- The total polyunsaturated fatty acid content of bison intramuscular tissue was greater than that of sheep.
- The ratio of PUFA to SFA was greater in bison intramuscular tissue than that of sheep.
- Greater amounts of CLA *c*-9, *t*-11 was found in sheep than in bison.
- Omega-6 and omega-3 fatty acid contents were greater in bison than in sheep.

- The ratio of omega-6 to omega-3 fatty acids was similar between bison and sheep.

The nutritional qualities of forage fed bison and sheep, in regards to their polyunsaturated fatty acid profiles, seem to be quite similar. Both bison and sheep have similarly ratios of omega-6 to omega-3 fatty acids in the range of 1.5-2:1 as a result of high forage diets. However, the increased amounts of saturated fatty acids found in sheep intramuscular tissue, most likely as a result of marbling fat deposits, is the key point that separates the two species. From a human health perspective, it would appear that bison would provide a more desirable fatty acid composition, hence yielding more lipid based health benefits than sheep.

6.0 General Summary and Conclusions

As the number of bison finished within western Canada grows, the interest in the nutritional qualities of bison meat will grow. Initial investigations found bison finished on forage to have a more favorable fatty acid profile than their feedlot finished counterparts from a human dietary perspective (Marchello and Driskell 2001). One of the objectives of this study was to observe the effect of diet type on the fatty acid profile of tissues from four commercial bison finishing programs. Conclusions drawn from this study include:

- High forage diets, as with the Forage Fed bison treatments, resulted in tissue containing greater amounts of polyunsaturated fatty acids, both of the omega-3 and the omega-6 fatty acid groups.
- Short term or low level supplementation with concentrates had a significant impact on the overall fatty acid profile of intramuscular tissue as indicated by the lower proportions of omega-3 fatty acids in intramuscular tissue of the <90 Day and 50:50 Forage:Grain treatments, as compared to the Forage Fed treatment.
- High concentrate diets, as with the Feedlot Finishing treatment resulted in the lowest levels of beneficial polyunsaturated fatty acids, and the lowest polyunsaturated to saturated fatty acid ratio amongst the bison treatments.
- Based on the ratio of polyunsaturated to saturated and omega-6 to omega-3 fatty acids, findings indicate that Forage Fed bison provide the most desirable ratio of beneficial fatty acids of the bison treatments from a human health perspective.

A secondary objective of this study was to compare bison to other ruminant species traditionally finished in western Canada. Intensively fed commercially finished bison bulls were compared to intensively fed steers and wethers finished on traditional western Canadian diets. Observations obtained from the study include:

- The total saturated fatty acid content of intramuscular tissue was similar among species, but bison contained the lowest levels of and myristic acid and the hypercholesterolemic fatty acid, palmitic acid.
- The PUFA to SFA ratio of bison intramuscular tissue was nearly twice of that of beef or sheep intramuscular tissue.
- The polyunsaturated fatty acid content of the intramuscular tissue was greater in bison than in beef or sheep for both the omega-6 and omega-3 fatty acid groups
- The ratio of omega-6 to omega-3 fatty acids was the lowest for bison (4:1) and the highest for beef (6:1), with sheep being intermediate (5:1).

Based on these findings, feedlot finished bison tissue contained a higher proportion of beneficial fatty acids while having a lower proportion of fatty acids shown to have detrimental effects on human health. No definitive conclusions can be drawn from the feedlot finishing comparisons of species, as the level of finish each species achieved prior to slaughter may have confounded the results.

Extensive forage finishing of ruminant species is popular around the world. However, traditionally only forage finished bison and sheep are common in western Canada. Conclusions drawn from the comparisons between forage finished bison bulls and sheep wethers include:

- Total saturated fatty acid content within intramuscular tissue was greater in sheep than in bison, but was similar for subcutaneous and perirenal tissue.
- Both myristic and palmitic acid content were greater in sheep intramuscular tissue than in bison intramuscular tissue.
- Bison contained a greater proportion of stearic acid within perirenal and subcutaneous tissue, but was similar to sheep with respect to the intramuscular tissue.
- Total polyunsaturated fatty acid content of bison intramuscular tissue was greater than that of sheep intramuscular tissue.
- The ratio of PUFA to SFA was greater in bison intramuscular tissue than in sheep intramuscular tissue.

- Greater levels of CLA *c*-9, *t*-11 was found in sheep than in bison.
- Omega-6 and omega-3 fatty acid content was greater in bison than sheep.
- The ratio of omega-6 to omega-3 fatty acids was similar between bison and sheep.

Forage fed bison and sheep had similar polyunsaturated fatty acid profiles. Bison and sheep had similarly low ratios of omega-6 to omega-3 fatty acids in the range of 1.5-2:1 as a result of being fed high-forage diets. However, the higher amount of saturated fatty acids found in the sheep intramuscular tissue, most likely as a result of marbling fat deposits, was a key point separating the two species. The lower proportions of cholesterol raising saturated fatty acids would favor bison intramuscular tissue over sheep on the basis of human health attributes.

In conclusion, comparisons of tissues indicated the highest level of polyunsaturated fatty acids to be located in intramuscular tissue. Subcutaneous and perirenal tissue contain greater proportions of saturated and monounsaturated fatty acids, with lower levels of polyunsaturated fatty acids.

Comparisons of finishing practices amongst species would favor the fatty acid profile of bison tissue under both intensively finished feedlot and extensive forage fed programs. Bison showed a greater proportion of fatty acids known to have a positive impact on human health while having lesser proportions of saturated fatty acids known to have negative impacts on human health. Preference for bison is a direct result of the comparisons made among bison and beef, and/or sheep under intensive or forage finishing conditions. Confounding factors such as management and degree of finish achieved by each species prior to slaughter must be taken into account when interpreting the final conclusions.

Finishing practices amongst bison would favor the Forage Fed treatment, followed by the 50:50 Forage:Grain, then the <90 Day Fed, with the Feedlot Finishing treatments in order based on the proportion of desirable fatty acids, in particular the content of omega-3 fatty acids, and the proportion of undesirable fatty acids such as myristic and palmitic acid.

7.0. Future Research Directions

From the findings presented within this thesis, future research directions for bison and other ruminant production, toward the pursuit of functional foods are suggested as follows:

1. Further investigations into maximizing forage and supplementary feed intake during finishing phases by capitalizing on compensatory gains in the spring and summer through intensive grazing management on either irrigated or fertilized paddocks

2. Comparison of bison production and meat quality from forage finished bison grazed or fed cool season forages, legume, green cereal crops, or unconventional plant species.

3. Formulate feedlot feeding programs to mimic meat fatty acid profile from forage finished animals through the use of oilseeds and fresh cut forages.

4. Enhancement of forage finished bison product by supplementation of grazing bison with high α-linolenic supplements.

5. Supplementation of bison calves while on pasture during their first fall and winter with high α-linolenic supplements to maximize omega-3 intake during peak growth phase.

6. Development of winter diet supplements that will mimic fatty acid intake from fresh forage.

7. Continue to study bison bulls in a low intensive production system, without use of hormonal implants or inclusion of ionophores within the diet. Available information into the effects of finishing programs on the fatty acid profile of bison tissues is limited and would benefit from further, more structured studies into the effects of contemporary feeding practices

8. Further investigations into how photoperiod affects bison metabolism and feed intake, and how to use that as a management tool.

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Appendix A. Identification of fatty acid by chain length, commo
name, and omega family

Chain Length[z,y]	Common Name	Omega Family
14:0	myristic	
14:1 *c*-9	myristoleic	
15:0	pentadecanoic	
16:0	palmitic	
16:1 *c*-9	palmitoleic	
17:0	margaric	
17:1 *c*-9	heptadecenoic	
18:0	stearic	
18:1 *t*-9	elaidic	
18:1 *t*-11	*trans* vaccenic	
18:1 *c*-9	oleic	
18:1 *c*-11	vaccenic	
18:2 *c*-9, 12	linoleic	Omega-6
20:0	arachidic	
18:3 *c*-6, 9, 12	γ-linolenic	Omega-6
20:1 *c*-11	eicosenoic	
18:3 *c*-9, 12, 15	α-linolenic	Omega-3
18:2 *c*-9, *t*-11	CLA	
18:2 *t*-10,*c*-12	CLA	Omega-6
20:2 *c*-11,14	eicosadienoic	Omega-6
22:0	behenic	
20:3 *c*-8,11,14	homo-γ-linolenic	Omega-6
20:3 *c*-11,14,17	eicosatrienoic	Omega-3
22:1 *c*-13	erucic	
20:4 *c*-5,8,11,14	arachidonic	Omega-6
22:2 *c*-13,16	docosadienoic	Omega-6
20:5 *c*-5,8,11,14,17	eicosapentaenoic	Omega-3
24:0	lignoceric	
22:4 *c*-7,10,13,16	docosatetraenoic	Omega-6
22:5 *c*-7,10,13,16,19	docasapentaenoic	Omega-3
22:6 *c*-4,7,10,13,16,19	docosahexaenoic	Omega-3

[z] *c*, *t* denote cis or trans configuration of double bond
[y] numbers following *c* or *t* indicate position of double bond fron
carboxyl group